Bulletin of the
British Ornithologists' Club

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FORTHCOMING MEETINGS

See also BOC website: **http://www.boc-online.org**

BOC MEETINGS are open to **all**, not just BOC members, **and are free**.

Evening meetings are in **an upstairs room at The Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE**. The nearest Tube stations are Victoria and St James's Park; and the 507 bus, which runs from Victoria to Waterloo, stops nearby. For maps, see http://www.markettaverns.co.uk/the_barley_mow.html or ask the Chairman for directions.

The cash bar opens at **6.00 pm** and those who wish to eat after the meeting can place an order. **The talk will start at 6.30 pm** and, with questions, will last *c*.1 hour.

It would be very helpful if those intending to come can notify the Chairman no later than the day before the meeting.

Tuesday 22 September 2015—6.30 pm—Dr Hazel Jackson—*Molecular phylogeography and mechanisms of invasion success in Ring-necked Parakeets across Europe*

Abstract: Invasive species present a major threat to global biodiversity; therefore understanding genetic patterns and evolutionary processes that enable successful invasions is paramount. Among birds, Ring-necked Parakeet *Psittacula krameri* is one of the most successful invasive species, established in over 35 countries. However, little is known about the ancestral origins of this species and what population genetic signatures tell us concerning their patterns of invasion. Evolution and genetic diversity in Ring-necked Parakeet populations is examined across Europe, alongside data on trade, climate and population growth, to highlight how multiple introductions and patterns of climate matching between the native and invasive ranges act as mechanisms for invasion success.

Biography: Hazel Jackson is a post-doctoral researcher with the Durrell Institute of Conservation and Ecology (DICE), at the University of Kent in Canterbury. Her research interests include evolution and population genetics of both endemic and invasive birds, in particular parrots. Hazel recently completed her Ph.D., which examined the evolution and ancestral origins of invasive Ring-necked Parakeets, whilst aiming to understand underlying genetic mechanisms that have enabled this species to become one of the most successful avian invaders around the globe.

Saturday 21 November 2015—One-day joint meeting on Bird Monitoring in the Middle East with Ornithological Society of the Middle East (OSME) and Natural History Museum (NHM) in the Flett Theatre, Natural History Museum, London SW7 5BD. The nearest tube station is South Kensington and attendees should use the NHM entrance on Exhibition Road. There is no charge to attend and all are welcome. The programme is planned to comprise:

Overview of BirdTrack for monitoring—Stephen McAvoy
Bird monitoring and Key Biodiversity Areas in Iraq—Richard Porter
Establishing long-term raptor monitoring in Turkey—Engin Yilmaz
Monitoring waterbirds at Lake Tengiz, Kazakhstan—Holger Schielzeth
Establishing shorebird monitoring and developing capacity in Kuwait—Gareth Bradbury & James Darke
Monitoring illegal bird killing in Cyprus—Bob Elliot

Access to NHM is possible from 10 am, when coffee/tea will be available adjacent to the Flett Theatre. The meeting will begin at *c*.10.30 am, with a break for lunch around 12.30 pm—many food outlets are available both within NHM and nearby in South Kensington. The afternoon session will begin at *c*.2 pm and, including a half-hour break for coffee/tea, should finish by 5 pm. NHM closes at 6 pm. For additional up-to-date details, please check the BOC website: http://www.boc-online.org

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Bulletin of the
BRITISH ORNITHOLOGISTS' CLUB

CLUB ANNOUNCEMENTS

ANNUAL GENERAL MEETING

The Annual General Meeting of the British Ornithologists' Club was held in the upstairs room at the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE, on Tuesday 19 May 2015, with Chris Storey in the Chair. Sixteen members were present.

1. **Apologies for absence** were received from David Fisher.

2. **Minutes of AGM 2014.** The Minutes of the 2014 AGM held on 20 May 2014 which had been published (*Bull. Brit. Orn. Cl.* 133: 165–166, and on the BOC website) were approved and signed by the Chairman.

3. **Chairman's Review, Bulletin Editor's Report, Trustees' Report and Accounts for 2014.** Copies of the document were available at the meeting. The Chairman began by thanking David Montier, who has retired as *Hon. Treasurer*, for his considerable contribution over the years to the Club. He added that he was delighted that Richard Malin had been elected at a Special General Meeting on 23 September 2014 to succeed David as *Hon. Treasurer.* The Chairman also thanked the Committee members, in particular David Fisher and Richard Langley, whose terms of office would end at the completion of the AGM. He also thanked Guy Kirwan, Eng-Li Green and Steve Dudley for their support and work during the past year. He concluded by noting that since the Annual Report went to press the Committee had held further discussions about the future of the Club and agreed that whilst efforts could be made to reduce costs, etc., and preserve the present *modus operandi* of the BOC, a successful outcome of this endeavour was far from certain and did not address the decline in membership, nor how best the BOC might operate in the 21st century.

The Committee had reached the view that the BOC would only survive if it took imaginative and bold initiatives in the light of the profound digital changes affecting both academic publishing and society in general. Therefore, rather than managing an inevitable slow decline, it was proposed that the BOC should adopt a radically different approach to deliver its principal mission. The Committee suggests that by embracing the digital revolution the BOC should be able to establish a coherent plan for the future, broaden its 'reach' and increase the dissemination of current taxonomic thinking to a larger potential audience. The BOC could become an online only organisation and the Bulletin an open-access publication. However, many details needed to be considered and a working group has been established to produce a detailed proposition, which would then be put to members for comment prior to any formal proposal for change. In answer to views from the floor, Pat Sellar and Tony Statham indicated their support for such an initiative.

The *Hon. Treasurer* reported that the result for the year showed a small surplus (of around £1,000) compared to an overall deficit of around £6,000 in 2013. This improvement largely stemmed from reduced printing costs and an increase in investment income. Income from subscriptions had continued to decline, but the cost of membership administration had risen. The Club has substantial investments, the value of which increased to more than £420,000 by the year-end, and this provides BOC with a strong base from which to address the membership cost challenge and to contemplate an online future.

Vol. 134 comprised 336 pages and 35 papers of broad geographical scope, although contributions on Neotropical birds remained particularly well represented. Taxonomy and nomenclature are Bulletin mainstays, and taxonomic papers on the genus *Pitohui*, Three-striped Warbler *Basileuterus tristriatus*, Cuban Bullfinch *Melopyrrha nigra*, Blackish Antbird *Cercomacra nigrescens*, Grey-headed Bristlebill *Bleda canicapillus*, Scaled Ground Cuckoo *Neomorphus squamiger* and McConnell's Flycatcher *Mionectes macconnelli* were published during the course of 2014. For the first time since 2004, no new taxa were proposed in the Bulletin's pages this year. For papers published in 2014, the interval between receipt and publication was 4–23 months, with a mean of *c.*11.4 months. The Bulletin received a total of 37 new manuscripts in 2014. Of these, six have been rejected to date and the rest have been accepted or are still being refereed for potential publication.

4. **Election of Trustees.** Nigel Redman was elected as Vice-Chairman (*vice* David Fisher). The meeting also elected Stephen Chapman and Alick Simmons (*vice* Richard Langley) to serve as Trustees.

5. **Any Other Business.** On behalf of the Club, the Chairman presented David Montier with a gift in recognition of his very special work for the BOC.

The 980th meeting of the Club was held on Tuesday 19 May 2015 in the upstairs room at the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE. Fourteen members and nine non-members were present. Members attending were: Miss H. Baker, Mr K. F. Betton, Mr M. Gauntlett, Mr G. M. Kirwan, Mr R. R. Langley, Mr R. W. Malin, Dr C. F. Mann, Mr D. J. Montier, Dr R. Prŷs-Jones, Mr N. J. Redman, Mr P. Sellar, Mr A. Simmons, Mr S. A. H. Statham, and Mr C. W. R. Storey (*Chairman*).

Non-members attending were: Ms K. Duke, Mrs M. Gaunlett, Mr P. Hollom, Dr H. McGhie (*Speaker*), Mrs M. Montier, Mr A. Richford, Mrs J. Storey, Ms D. Summers.

Dr Henry McGhie, Head of Collections and Curator of Zoology at Manchester Museum, spoke on *Who do you think you are, Henry Dresser? Birds, books and business*. Henry Dresser was one of the most important British ornithologists of the 19th and early 20th centuries. 2015 marks the centenary of his death, but just who was he and what did he do? Viewed from the present perspective, with well-formed science institutions and societies, it is difficult to imagine how a band of independent-minded men banded together to shape the institutions we have today. Henry Dresser and his contemporaries embraced the Victorian ideal of self-help, and took full advantage of their opportunities to further their personal interests. Dresser was born in Yorkshire and his father worked as a merchant dealing in Baltic timber. Henry was educated to assume the family business and travelled very widely in northern Europe from the age of 14; he also spent time in New Brunswick, and in Texas during the American Civil War. Wherever he went, he furthered his bird skin and egg collection (a must-have for any serious 19th century ornithologist), using business trips as an opportunity to meet curators, naturalists and collectors overseas.

When he settled down in London, in his late twenties, Henry and his ornithologist friends collaborated closely, building their own specialist collections and mixing in scientific society. Dresser specialised in Palearctic birds and his collections helped produce the eight-volume *History of the birds of Europe*, begun with Richard Bowdler Sharpe of the British Museum. Henry went on to produce several other important reference books: monographs on rollers (Coracidae) and bee-eaters (Meropidae), a condensed manual of Palearctic birds, and another work on European birds' eggs. He was a 'mover and shaker' in the development of early bird protection laws, and a leading light in the early Society for the Protection of Birds (now the Royal Society for the Protection of Birds), as well as in the British Ornithologists' Union and Zoological Society of London. Henry's collections are now mostly in the Manchester Museum. Dresser's life will form the subject of a book, due to be published in 2017.

'Bogotá' type specimens of the hummingbird genus *Adelomyia*, with diagnosis of an overlooked subspecies from the East Andes of Colombia

by Thomas M. Donegan & Jorge Enrique Avendaño

SUMMARY.—Molecular work has revealed that Speckled Hummingbirds *Adelomyia melanogenys* in the East Andes of dpto. Santander, Colombia, represent a distinct lineage not previously recognised taxonomically. Most specimens from this region differ from others taken in the East Andes by their more extensively rufous and speckled posterior underparts. Sound-recordings and biometrics showed broad overlap for all variables in both populations. Statistically significant but non-diagnosable differences exist in the number of notes in trills of songs, speed of calls and bill length. The type of *Adelomyia melanogenys* (Fraser 1840) is a 'Bogotá' specimen similar to birds from dpto. Cundinamarca, Colombia. *Trochilus sabinae* Bourcier & Mulsant, 1846, is also based on a 'Colombia' specimen. A possible type was identified that resembles the Santander population in its underparts. *Adelomyia simplex* Boucard, 1893, is based on a leucistic 'Bogotá' specimen more consistent with the Cundinamarca population than others. If the Santander population is recognised taxonomically, it is suggested to clarify the type locality for *sabinae* as the west slope of the East Andes in Santander or Boyacá, but molecular work is needed to confirm this. *A. m. inornata* in the southern Andes has a faster call and distinctive plumage, and perhaps merits species rank.

The genus *Adelomyia* is monospecific, comprising the polytypic Speckled Hummingbird *A. melanogenys*, a widespread Andean hummingbird. The following names have been recognised as valid subspecies, with type localities in parentheses: *maculata* Gould, 1861 (Quito), *chlorospila* Gould, 1872 (San Antonio, Peru), *aeneosticta* Simon, 1889 ('Venezuela'; considered by Cory 1918 to be near Mérida), *cervina* Gould, 1872 (Medellín, Central Andes, Colombia), *inornata* Gould, 1846 (Sandillani, Yungas, Bolivia), *connectens* Meyer de Schauensee, 1945 (head of Magdalena Valley at La Candela, dpto. Huila, Colombia) and *debellardiana* Aveledo & Perez 1994 (Venezuelan side of Perijá Mountains) (Dickinson & Remsen 2013). The names *melanogenys* Fraser, 1840, *sabinae* Bourcier & Mulsant, 1846, and *simplex* Boucard, 1893, are all based on 'Bogotá' or 'Colombia' trade specimens, the latter two being generally regarded as synonyms of the first.

Molecular studies have revealed that birds on the west slope of the East Andes in dpto. Santander to northern dpto. Boyacá (hereafter 'Santander–Boyacá population') differ in mtDNA from all other north Andean populations (Chaves & Smith 2011, Chaves *et al.* 2011). Differences are substantial: 5.8% versus other populations in the East Andes with which the Santander–Boyacá population has historically been treated as consubspecific (Chaves & Smith 2011: 7, Table 2). These studies were based on sequences of five specimens at Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH). We studied the sequenced specimens and others from the region, analysed vocal and biometric data, and considered the phenotypic differentiation and names for the Santander–Boyacá population.

Figure 1. Post-1997-collected specimens of (above) main East Andes population and (below) Santander–Boyacá population. Top row: (i) ICN 33152 (El Retiro, Ubalá, dpto. Cundinamarca); (ii) ICN 33951 (Toledo, Parque Nacional Natural Tamá, dpto. Norte de Santander); (iii) ICN 34757 (Santa María, dpto. Boyacá); (iv) ICN 22366 (La Aguadita, dpto. Cundinamarca); (v) ICN 33154 (as i); bottom row: (i) ICN 34816; (ii) ICN 34364; (iii) ICN 36458; (iv) ICN 35820; (v) ICN 34987, details of which appear in Appendix 3 (T. M. Donegan)

Figure 2 (left). ICN 33152 (Cundinamarca) and ICN 35828 (Santander) showing differences in underparts coloration; for details of specimens see Fig. 1 (T. M. Donegan)

Figure 3 (below): IAVH series of the Santander–Boyacá population, from left to right: 10293, 13446, 13463, 10562, 8331, 8336; details of specimens in Appendix 3 (T. M. Donegan)

Methods

Adelomyia songs typically commence with a very fast rising trill, comprising short notes over a broad frequency, followed by stronger, slower notes with thicker maxima and terminal downstrokes, each of progressively lower max. frequency (Fig. 4, hereafter 'song'). The species also gives repeated single, high-pitched *chit* notes over a relatively narrow bandwidth (Fig. 5, hereafter 'call'). Sonograms were produced of songs and calls of the Santander–Boyacá population (n = 18 songs from 13 assumed individuals and n = 7 calls from seven individuals) and those from elsewhere in the East Andes north of the Andalucía Pass between dptos. Huila and Caquetá near Parque Nacional Natural Serranía de los Picachos (n = 21 songs from 11 individuals and n = 5 calls from three individuals). Relatively few sound-recordings were available, despite the species' abundance in appropriate habitats, suggesting that it is not a very active songster or is infrequently recorded. For songs, total length and max. frequency were measured for the entire vocalisation. Number of notes, length and speed were then measured separately for the initial trill and later slower notes (Appendix 2). In some recordings, intermediate notes with both broad bandwidth and a longer terminal element occur, making the distinction between the trill and longer notes less obvious. In such recordings, different parts of songs were separated based on the point before where a note with strong terminus and longer gap preceding it first appears. Some songs included only the trill or the longer notes, but not both; these were excluded from analyses. Calls are typically very long and many recordings are only of fragments. As a result, a 3–16-second sample (depending on the length of the recording) was taken. Number of notes and length were measured to permit speed to be calculated. The max. and min. acoustic frequency of a typical note were then measured for each recording, and used to calculate note bandwidth. Short rattle calls are also given while foraging or in contact, or by birds in the hand in alarm, but these were not studied.

Biometric data were collated from mist-net surveys in Colombia reported in Donegan & Dávalos (1999) (West Andes: *cervina* / *ultracervina*), Salaman *et al.* (1999) (East Andes: *melanogenys* / *connectens*) and Donegan *et al.* (2007, 2010) and Villanueva & Huertas (2011) (Santander–Boyacá population). Biometric data for the latter and other East Andes populations (Norte de Santander, Cundinamarca and southern / eastern Boyacá specimens) were compared using specimens at IAvH and were also taken for putative type specimens.

The following statistical tests for diagnosability developed by Donegan (2008, 2012) and Donegan & Avendaño (2008) were applied to the vocal and biometric data.

LEVEL 1: statistically significant differences at $p<0.05$. A Bonferroni correction was applied (songs: eight variables each, $p<0.006$); calls four variables $p<0.013$; biometrics five variables $p<0.010$). An unequal variance (Welch's) t-test was used; for song speeds, a two-sample Kolmogorov-Smirnov test was applied as an additional test that must be satisfied for Level 1, to account for the possibility of a non-normal distribution. These calculations assess the statistical significance of differences between means of populations, but do not address diagnosability, as they tolerate considerable overlap.

Further calculations were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, $\bar{x}_1$ and s_1 are the sample mean and sample standard deviation of Population 1; $\bar{x}_2$ and s_2 refer to the same parameters in Population 2; and the t value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following one of Hubbs & Perlmutter's (1942) subspecies concepts, which is passed if sample means are two mean standard deviations or more apart
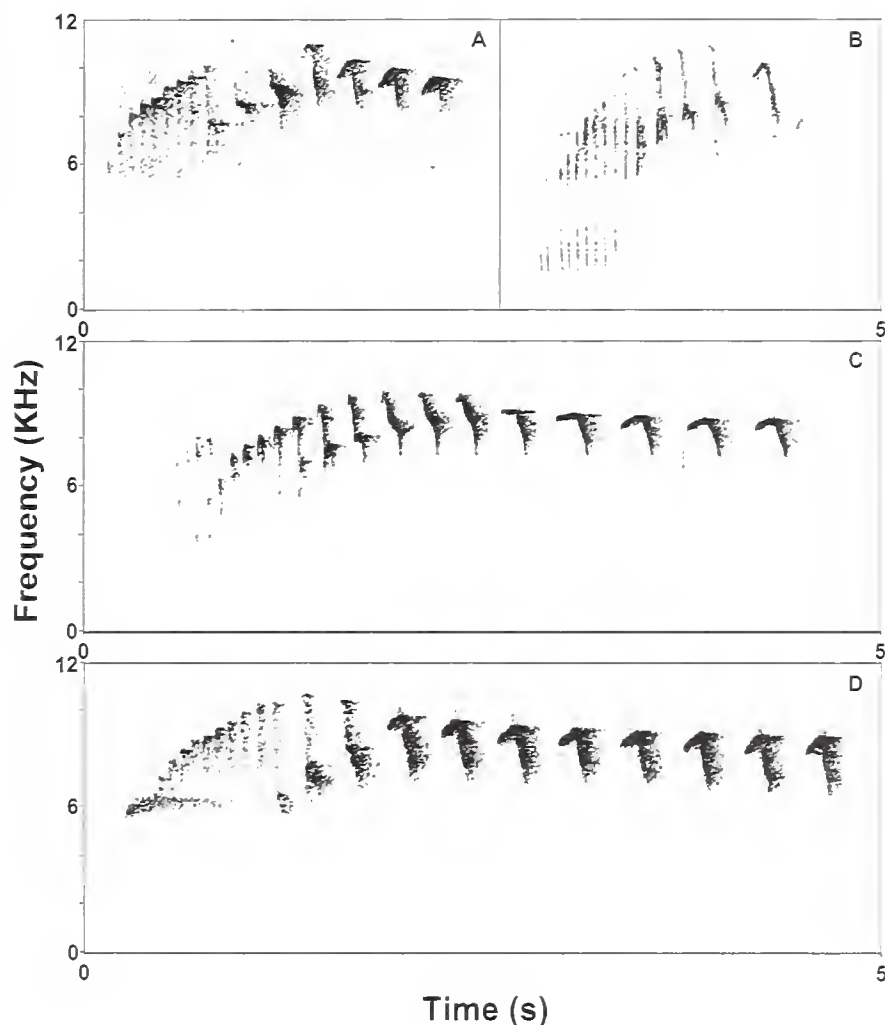
Figure 4. Songs of two Speckled Hummingbird populations in the East Andes of Colombia: Santander–Boyacá population (A–B) and nominate of East Andes (C–D). A: XC64410 (Yariguíes, dpto. Santander). B. XC12688 (north-western dpto. Boyacá). C. XC94059 (dpto. Cundinamarca). D. XC12340 (eastern dpto. Boyacá). For full details of localities and recordists, see Appendix 2.
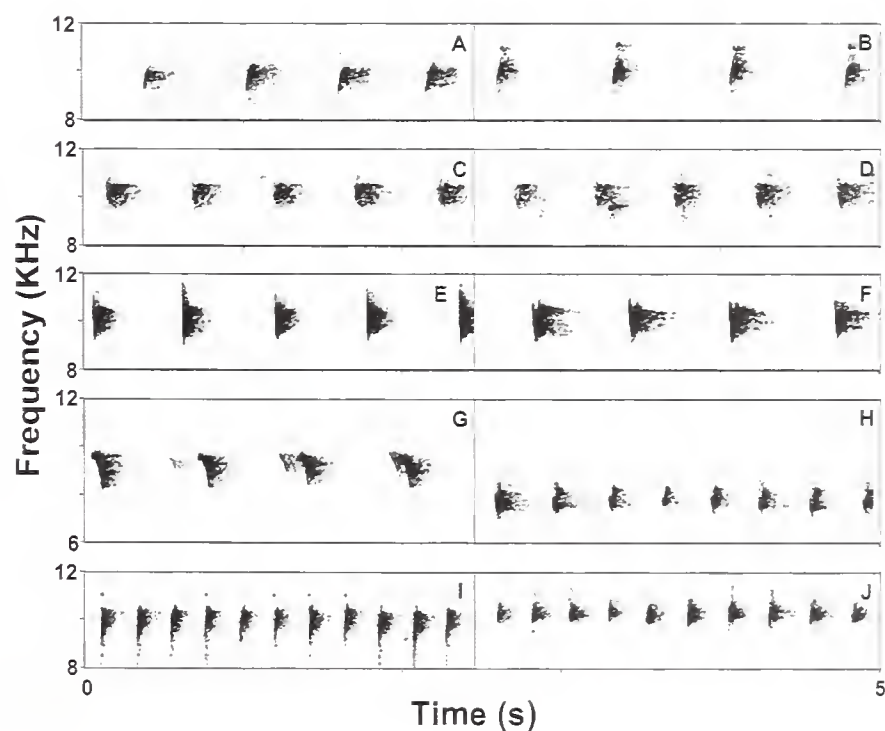
Figure 5. Calls of Speckled Hummingbirds at various Andean localities. Santander–Boyacá population (A–B), East Andes of Colombia (*melanogenys*: C–D), Ecuador (*maculata*: D; and *melanogenys* group: E–F), Peru (*melanogenys* group or *chlorospila*: G; and *chlorospila*: H) and Bolivia (*inornata*: I–J). A. XC246071 (Yariguíes, dpto. Santander: T. M. Donegan). B. XC18358 (north-western dpto. Boyacá: H. van Oosten). C. XC96255 (dpto. Meta: O. Cortés). D. XC89354 (dpto. Meta: O. Cortés). For details of A–D see Appendix 2. E. XC6702 (Tandayapa Valley, Pichincha, Ecuador: N. Athanas). F. XC126906 (Cordillera del Cóndor, Zamora-Chinchipe, Ecuador: L. Ordóñez-Delgado). G. XC5590 (Corral Grande, Zona Reservada Laquipampa, Lambayeque, Peru: W.-P. Vellinga). H. XC63097 (Cock of the Rock Lodge, Manu, Peru: J. Tobias & N. Seddon, response to playback). I. XC1712 (Chillaguatas, Tariquia, Tarija, Bolivia: S. Mayer). J. XC2930 (Carrasco National Park, Cochabamba, Bolivia: A. B. Hennessey)

controlling for sample size, i.e. the sample mean of each population falls outside the range of 97.5% of the other population: $|(\overline{\chi}_1 - \overline{\chi}_2)| > (s_1(t_{1\ @\ 97.5\%}) + s_2(t_{2\ @\ 97.5\%}))/2$.

LEVEL 3: The traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size, which requires both of the following tests to be passed: $|(\overline{\chi}_1 - \overline{\chi}_2)| > s_1(t_{1\ @\ 99\%}) + s_2(t_{2\ @\ 75\%})$ and $|(\overline{\chi}_1 - \overline{\chi}_2)| > s_2(t_{2\ @\ 99\%}) + s_1(t_{1\ @\ 75\%})$.

LEVEL 4: diagnosability based on recorded values or, for plumage and subjective vocal characters (note shape and change of note shape), subjective diagnosability; the first part of Isler *et al.*'s (1998) diagnosability test.

LEVEL 5: 'Full' diagnosability (where sample means are four mean standard deviations apart at the 97.5% level, controlling for sample size); the second part of Isler *et al.*'s (1998) diagnosability test: $|(\overline{\chi}_1 - \overline{\chi}_2)| > s_1(t_{1\ @\ 97.5\%}) + s_2(t_{2\ @\ 97.5\%})$.

The Tobias *et al.* (2010) scoring system was also considered. We do not expressly endorse this system, but use it as a reference point to evaluate taxonomic rank.

We also investigated possible type specimens for three available names in the genus *Adelomyia* based on 'Bogotá' or 'Colombia' type specimens: *Trochilus melanogenys* Fraser, 1840; *Trochilus sabinae* Bourcier & Mulsant, 1846; and *Adelomyia simplex* Boucard, 1893. No subsequent publication concerning the genus discusses any of the types of these names in detail, despite several studies (e.g. Cory 1918, Zimmer 1951, Schuchmann 1999, Chaves & Smith 2011, Chaves *et al.* 2011). Biomap Alliance Participants (2014), who databased all Colombian specimens in public museums worldwide, except IAvH, was used to locate types and other important specimens. We studied all *Adelomyia* in the American Museum of Natural History, New York (AMNH), Natural History Museum, Tring (NHMUK), IAvH, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN), Universidad Industrial de Santander, Bucaramanga (MHN-UIS), Muséum National d'Histoire Naturelle, Paris (MNHN) and US National Museum, Smithsonian Institution, Washington DC (USNM). We also obtained photographs from the World Museum, Liverpool (LIVCM). This review included examination of many historic 'Bogotá' or 'Colombia' specimens of *A. melanogenys*, at AMNH (n = 39), LIVCM (n = 2), MNHN (n = 6), NHMUK (n = 21) and USNM (n = 8).

Results

Biometric and vocal data are presented in Appendices 1–2. Statistically significant differences were found between the Santander–Boyacá population and the nominate in number of notes (Level 1, p=0.0003) and length (Level 1, p=0.005) of the trill part of the song. For calls, statistically significant differences in speed were found, which passed the first part of the Level 1 test based on Welch's t (p=0.011) but not when a Bonferroni correction is applied, using Kolmogorov-Smirnov (p=0.020). Data are also suggestive of average broader bandwidth for calls in the Santander–Boyacá population, but tests of significance were not met doubtless due to sample size. The difference in call speed is noteworthy given that this varies geographically, with *inornata* of Bolivia, which is sister to all other *Adelomyia* in the molecular phylogeny, being fastest (Fig. 5). Differences in bill length (p=0.05) also narrowly missed the Level 1 test of statistical significance when applying a Bonferroni correction. Bill measurements were considered to vary substantially between other *Adelomyia* populations by Chaves & Smith (2011), who did not study biometrics of the Santander–Boyacá population.

Twelve of the 16 Santander–Boyacá specimens with definite locality data (Appendix 1), including all Yariguíes material, are distinguishable from series collected elsewhere in the

East Andes, in having more extensive rufous (marked with glittering green speckles) on the flanks and belly-sides (Figs. 1–3). Their morphology is described in Appendix 4. West and Central Andes specimens (variously attributed to subspecies *cervina*, *ultracervina*, *connectens* or '*intergrediens*') have a more rufous ground colour to the throat and breast, with less contrasting striations on the throat. Venezuelan specimens (*aeneosticta*) show a yellower shade of glittering green on the ventral surface and a more contrasting and extensively white breast.

Taxonomic rank of the Santander–Boyacá population

Based on molecular studies, the Santander–Boyacá population is a phylogenetic species (Cracraft 1983). It would not meet the requirements for species rank under a comparative Biological Species Concept (*cf.* Helbig *et al.* 2002), given that *Adelomyia* is currently treated as monospecific. Ranking this population as a species would also require splitting *inornata*, *aeneosticta* and *maculata* (with *chlorospila*) to preserve monophyly. Applying Tobias *et al.* (2010), the Santander–Boyacá population would attain 1–2 points for coloration and speckling of its flanks and belly, one point for the number of notes in the trill part of the song and one point for call speed compared to *melanogenys* (total 3–4: less than the required seven for species rank). We suspect that one additional point would be awarded for bill length using a larger sample.

No consensus exists as to if or how avian subspecies should be recognised. Patten (2015) proposed that only a failure to achieve both phenotypic and genotypic distinctiveness should deny subspecies status, implying that distinct lineages such as this one should be recognised even in the absence of phenotypic diagnosability. Under their scoring system, Tobias *et al.* (2010) proposed a benchmark of seven points for species rank, which implies that 3–4 points could be an appropriate score for subspecies rank, especially in a genus where less ancient lineages are recognised taxonomically. In contrast, Remsen's (2010) proposed subspecies concept requires a single diagnosable character, which is lacking for the Santander–Boyacá population, unless molecular characters are considered.

Trochilus melanogenys

In the next three sections, we consider whether any names in *Adelomyia* based on East Andes specimens might apply to the Santander–Boyacá population. The name *melanogenys* was described from a 'Bogotá' specimen by Fraser (1840). Louis Fraser worked at the Zoological Society's Museum in Brewer Street, London. Specimens appear to have flowed regularly from him to the British Museum only from 1846 (E. C. Dickinson *in litt.* 2012). Earlier material—including the *melanogenys* type—would have been accessioned to the Zoological Society of London collection, which is no longer extant. One 'Bogota' specimen we examined (NHMUK 1887.3.22.1561) is annotated: 'Agrees with the type of *A. melanogenys* in the Liverpool Museum comp. 19 Mar 1890 O.S.' [Osbert Salvin]. Of two 'Bogotá' specimens at LIVCM (D1098 and D1098b), one D1098 (Fig. 7) bears a red holotype label and a label of the Mus. Derbianum of Liverpool also annotated 'type'. It was catalogued by Wagstaffe (1978) as the type, but its status has been overlooked in the hummingbird literature. The label is inscribed: '*Trochilus melanogenys* Fraser. Original of W. Fraser's description in the Proc. Zool. Soc. 1840 p. 18. From Sta. Fé de Bogotá' and on the reverse: '1841. Rec'd from Fraser Mar 31. Length 3¾ In. Extend 4¾ In.'.

The type's plumage is consistent with Fraser's (1840) description. In relation to the lower underparts, it reads: 'corpore subtus ex-ochreo-albo; abdominis lateribus rufo lavatis' ['underparts ochre-white; abdominal sides washed reddish']. That the sides (but

Figure 6. An individual of the Santander–Boyacá population of Speckled Hummingbird *A. melanogenys*. Páramo La Floresta, Serranía de los Yariguíes, Zapatoca, dpto. Santander, January 2011 (B. Huertas / Proyecto YARE II)

Figure 7. Type of *Trochilus melanogenys* (Liverpool museum D1098), showing the pale central vent typical of Cundinamarca birds (Clem Fisher & Tony Parker)

not undertail or belly) are washed rufous is a feature of birds from dptos. Cundinamarca and eastern Boyacá. Fraser (1840) gave both total length and wing length as 3¾ inches. It is implausible that an *Adelomyia* would have wing and total length equal: the wing length is presumably in error (*cf.* Appendix 1) and is not stated on the specimen label.

We propose to clarify the type locality of *melanogenys* as the west slope of the East Andes south of dpto. Boyacá or the east slope of the East Andes south of dpto. Norte de Santander, i.e. that part of the East Andes of Colombia within the range of Clade D of Chaves & Smith (2011: Fig. 1b) and Chaves *et al.* (2011: Fig. 5).

Trochilus sabinae

Trochilus sabinae Bourcier & Mulsant, 1846, is based on a specimen from 'Bogotá, dans la Nouvelle-Grenade'. The spelling '*sabinae*' was used in the original description. David & Peterson (2010) endorsed using original spellings for various Bourcier names originally described as unmodified personal names, but *sabinae* was described in this Latinised form.

In the original description, *sabinae* is not distinguished from *melanogenys*, suggesting its authors were either unaware of Fraser's (1840) earlier description or had not made the connection. The description fits a Speckled Hummingbird. Its underparts are described: 'Parties plus postérieures du dessous du corps d'un blanc sale sur la région longitudinalement médiaire, d'un blanc fauve ou d'un fauve pâle sur les côtés, et plus densement et plus visiblement marqué sur ceux-ci que sur celle-là de mouchetures d'un vert semi-doré.' [More posterior parts of the underparts dirty white on the medial line, of a fawn-white or pale fawn on the sides, and more densely and more clearly marked thereon with flecks of semi-golden green.] Measurements (total length 92 mm, bill 16 mm, wings 54 mm, rectrices 38 mm) are given. No illustration accompanies the description and no specimens are cited.

Bourcier & Mulsant's (1846) name was used by Reichenbach (1855) (who omitted *melanogenys*) as *Metallura sabinae*. Bonaparte (1854) placed *sabina* (an incorrect subsequent spelling of *sabinae*), *inornata* and Blossomcrown *Anthocephala floriceps* in a new genus *Adelomyia*. *Trochilus sabinae* was later designated from among these names as the type species of *Adelomyia* by Gray (1855). (Cory 1918 incorrectly stated *melanogenys* to be the type species of this genus.) Gould (1861), Mulsant *et al.* (1866), Mulsant & Verreaux (1877), Elliot (1879), Boucard (1893), Hartert (1900), Cory (1918) and Zimmer (1951) all treated *sabinae* as a junior synonym of *melanogenys*. The genus *Adelisca* Cabanis & Heine, 1860, has as its type species *melanogenys* and is generally treated as a junior synonym of *Adelomyia* Bonaparte, 1854.

Many hummingbird types designated by Bourcier (alone or co-authored with Mulsant, De Lattre or Verreaux) reached Elliot's collection (e.g. Elliot 1879) and were transferred to AMNH, including the supposed types of *Trochilus antoniae* Bourcier & Mulsant, 1846 (=*Threnetes niger*), *Trochilus franciae* Bourcier & Mulsant, 1846 (=*Amazilia franciae*), *Trochilus corallirostris* Bourcier & Mulsant, 1846 (=*Amazilia rutila corallirostris*), *Trochilus viridipallens* Bourcier & Mulsant, 1846 (=*Lampornis viridipallens*) and *Trochilus rosae* Bourcier & Mulsant, 1846 (=*Chaetocercus jourdanii rosae*). Various Bourcier types were examined at AMNH. Most are mounted and have colourful more or less square labels written in red and blue ink denoting their status.

Greenway (1978: 3) considered that some of Bourcier's types lack type specimen labels, which may have been removed. Bourcier's specimens were regularly exchanged with other hummingbird collectors of the time. As an indication of the widespread trade in such specimens at the time, Mulsant *et al.* (1866) includes an advertisement by W. Schlüter for hummingbirds and other specimens, with *A. melanogenys* among the cheapest at 1.5 marks

Figure 8. Possible *Trochilus sabinae* type (MNHN 347), Muséum National d'Histoire Naturelle, Paris (T. M. Donegan)

(vs. up to 40 marks for a Red-tailed Comet *Sappho sparganurus* or 160 marks for the most expensive bird-of-paradise). To compound matters, Bourcier sometimes specified 'type' on specimens that were representative of the species but not actual types (Greenway 1978: 5).

The current whereabouts of some of Bourcier's types is a mystery. Deslongchamps (1881) queried whether Elliot (who later deposited specimens at AMNH) certainly obtained the types of *Trochilus grayi*, noting that the Bourcier collection was dispersed at a public sale after his death, and that the Faculty of Sciences of Caen obtained some specimens of this species (along with other Bourcier specimens). It is probable that most of the Caen collection was destroyed during World War II (Greenway 1978: 4). However, Deslongchamps (1881) did not mention any *Adelomyia* in his Caen museum catalogue, so this does not seem a likely repository of the *sabinae* type. Jardine (1852) reported that a collection of Bourcier's, purchased by Dr Edward Wilson of Philadelphia was lost at sea. It is unknown whether this collection included the *sabinae* type.

Among a large collection of *Adelomyia*, MNHN has five specimens each bearing a more or less square label attached with pink string annotated 'G. *Adelomyia sabina*', with 'sabina'
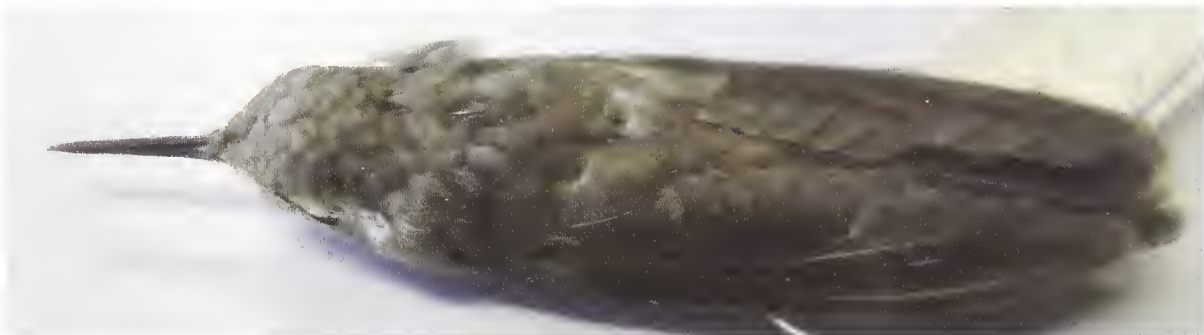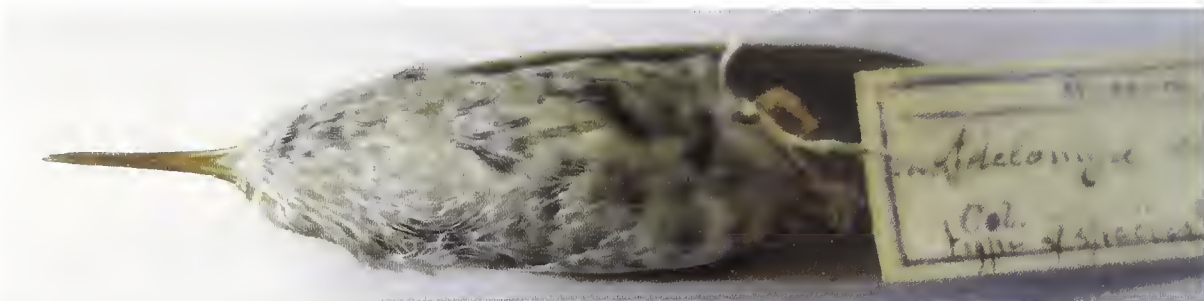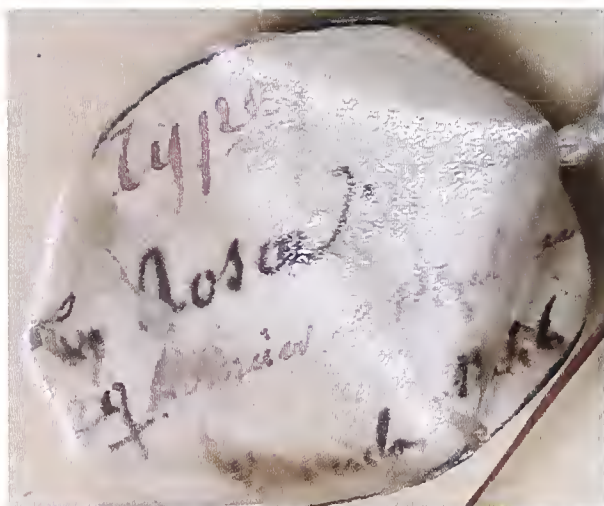
Figure 9 (above and left). Dorsal and ventral views of type of *Adelomyia simplex* (MNHN CG1989.398), Muséum National d'Histoire Naturelle, Paris, with close-up of head (T. M. Donegan)

Figure 10 (below). Label on the Bourcier type of *Trochilus rosae*, American Museum of Natural History, New York (T. M. Donegan)

then crossed out for *melanogenys*. None of the other specimens of *melanogenys* studied by us bear labels with the name *sabinae*, 'sabine' or 'sabina'. Two of the MNHN specimens (1896-353, 1896-354) were collected near Caracas, Venezuela, and accessioned from Levraud (French consul in Caracas) in the year specified. They are of subspecies *aeneosticta*, morphologically and by locality. Both specimens post-date the description of *sabinae*. As Levraud presumably donated locally sourced specimens to MNHN, the pink-stringed label was probably attached at MNHN. Two other 'sabina' specimens have similar labels, are unnumbered and lack locality data or additional information.

The final 'sabina' specimen, MNHN 347 (Fig. 8), has an additional handwritten label annotated 'sabine' and another 'P. Mr. Lewy 1850' with 'No. 347'. The 'P' on Lewy specimens has been considered a contraction of 'presented' (e.g. Hellmayr & Conover 1942). MNHN 347 was therefore presented to or by Lewy just four years after the description of *sabinae*.

Unlike the Bourcier types at AMNH, MNHN is unmounted and lacks ornate, colourful labels (*cf.* Fig. 10). We compared the handwriting in the name 'sabine' on the label of MNHN 347 with that on the labels on types of contemporaneously described species, including

Figure 11. Other type specimens of names in genus *Adelomyia*, left to right: (i) *inornata*; (ii) *maculata*; (iii) *cervina*; and (iv) *chlorospila*, all at Natural History Museum, Tring (T. M. Donegan)

Trochilus rosae Bourcier & Mulsant, 1846 (=*Chaetocercus jourdanii rosae*) and *Trochilus franciae* Bourcier & Mulsant, 1846 (=*Amazilia franciae*). Most are written in a calligraphic style that was relatively widespread in the mid 1800s. The original labels of AMNH types are more ornate and written in three different colours for each of the species name, the word 'type'

and the authors. However, there are notable similarities. In particular, the 's' is of quite similar shape on the 'rosa' and 'sabine' labels (although one is upper and the other lower case), both are slanted and in both the final letter is embellished by a line at the end, which in the word 'rosa' is upturned (Fig. 10). The name 'franciae' on the original label is written with letters less connected than on the 'sabine' label (writing more slowly or carefully). The lack of a more ornate Bourcier label on MNHN 347 or such careful handwriting could be explained by the name *sabinae* being in synonymy with *melanogenys* and its type specimen then being sold or neglected. Some other supposed AMNH Bourcier types, e.g. *Eriocnemis derbyi*, lack these sorts of labels. Also notable is that the unmodified names 'rosa' and 'sabine' are used on the labels in both cases. This reflects Bourcier & Mulsant's (1846) French vernacular name 'Le C. de Sabine', which continued to be used for *A. melanogenys*, following its synonymy, by Mulsant & Verreaux (1877) as 'L'Adélomye de Sabine'.

Measurements of MNHN 347 are remarkably similar to those of the type in the original description. Bill to skull is 19 mm, but the bill to feathers length is identical to that in the description (16 mm). Wing is 51.5 mm, 2.5 mm shorter than in the description, but 4% shrinkage in wing length can be expected over *c.*165 years (Winker 1993) and differing measuring protocols could also be responsible. Tail is almost identical in reported length at 37.5 mm. The bill is longer than that of the small sample of specimens measured from Santander, but within the range of the larger mist-net sample from this region and also within that for East Andes populations.

The *sabinae* type(s) might be one of the tens of other 'Bogotá' or 'Colombia' specimens in museums, or it could have been sold to a private collector or lost in the collection sold to Wilson. However, for the reasons above, MNHN 347 may be the type of *sabinae*.

MNHN 347 lacks some undertail-coverts and lower belly feathering, probably as a result of preparation and subsequent handling as one of the labels is attached very close to the legs. This makes any identification tentative, but MNHN 347 clearly has buffy feathers in the lower chest to undertail region, with rather large green discs on the sides close to the central belly, resembling Santander–Boyacá specimens most closely in this respect (Fig. 8; *cf.* Figs. 1–3).

The spellings 'sabina', 'sabine' and 'rosa' when used here are solely mentioned to discuss wording on specimen labels and French vernacular names, and are not proposed as emendations or valid subsequent spellings.

Adelomyia simplex

A. simplex was based on a 'Colombia' specimen. Boucard (1893) wrote: 'I have also one specimen with the upperside pale slaty-gray. Tail and wing brownish-gray. All the rectrices excepting the median tipped with buffy white. Underside whitish-gray, spotted with small brown spots on throat and flanks. If it should prove a distinct species, I propose the name of *Adelomya simplex* for it.' (The name *Adelomya* Mulsant & Verreaux, 1866 is an incorrect subsequent spelling of *Adelomyia* Bonaparte, 1854, which was relatively widely used in the 1800s.) The name *simplex* was considered a synonym of *A. melanogenys* by Hartert (1900). This name should not be confused with *Eriopus simplex* Gould, 1849, which is also based on a 'Colombia' trade specimen and which Cory (1918) considered to represent an 'abnormal phase of plumage' of Coppery-bellied Puffleg *Eriocnemis cupreoventris*.

The type of *A. simplex* is at MNHN (CG1989.398: Fig. 9). The specimen bears a 'Museum Boucard' label inscribed '*Adelomya simplex* type of species Columbia [*sic*]'. It had not previously been set aside in the type collection at MNHN but is now. The bill is yellowish below (rather than grey as in *melanogenys*) and more extensively pale, and its legs are also yellow. The bare parts are naturally this colour, not painted. The underside

is pale gray, with brown spots from the throat to breast and flanks. The lower belly and undertail are all white. Leucism is rare in *Adelomyia*, though we found a specimen of the nominate subspecies (NHMUK 2002.3.799, 'C.B.XXI.169', 'Columbia') with one all-white rectrix. There was a thriving trade in hummingbirds during the mid 1800s for the millinery business and whilst most specimens were used for such purposes, unusual ones were sold to private collectors.

Biometrics (bill to skull 17.2 mm, wing 55.5 mm, tail 38 mm), supercilium, throat and tail plumage and tail shape (only very slight fork) are broadly consistent with nominate *A. melanogenys*, although tail length is rather long for an old specimen of any population studied here (Appendix 1). Tail and throat to breast pattern (if not coloration) are also consistent with *Adelomyia*. Its subspecific identity should be confirmed genetically. It is presently impossible to refute the null hypothesis that this 'Bogotá' specimen originated from the environs of Bogotá, but we cannot eliminate the possibility it was collected elsewhere using morphology alone.

Other available names in *Adelomyia*, their status and taxonomic rank

Two other names are based on types in the Bonn museum (Schuchmann 1984, van den Elzen 2010, Dickinson & Remsen 2013): *ultracervinus* Kleinschmidt, 1943 (La Cumbre, Valle del Cauca) and *intergrediens* Kleinschmidt, 1943 (Río Toche, Quindío Pass and Cañón del Monte Tolima, 1,700–2,400 m, Colombia: Central Andes). The West Andes population is generally treated as consubspecific with *cervina* of the Central Andes. Specimens are similar in plumage and molecular data show no major distinction between these ranges. We presume that both of Kleinschmidt's (1943) names are junior synonyms of *cervina*, assuming that they are normal *Adelomyia* from the localities stated, but their type specimens should be verified to confirm this.

The names *cervina* and *chlorospila* were afforded species rank by Gould (1887) and some others. Argentine, Bolivian and Peruvian (Cuzco and Puno) populations referable to *inornata* were ranked as a species by Gould (1846, 1861, 1887), Mulsant & Verreaux (1877), Elliot (1879), Hartert (1900) and Cory (1918). However, the genus has been treated as monospecific essentially universally since Peters (1945), e.g. by Zimmer (1951), Schuchmann (1999), Schulenberg *et al.* (2007), Dickinson & Remsen (2013), Remsen *et al.* (2015). The southern populations differ from other *Adelomyia* in having bluish throat feathers, more rufous mantle and rump, and from most populations (but not *chlorospila*) in their buffy tail tip (Fig. 11). They also have a faster paced call than all congeners (Fig. 5). We have not analysed vocal differences statistically, due to the small sample of this type of vocalisation from Peru. Populations referable to *inornata* exceed the Tobias *et al.* (2010) benchmark for species rank, with at least three points for gorget coloration, two for rump and mantle coloration and three for call speed. Chaves & Smith (2011: Fig. 6) considered *inornata* not to differ significantly in biometrics from other populations, but it occupies different climatic and environmental space, resulting in one additional point. A total score of at least nine exceeds the seven suggested for species rank. Chaves & Smith (2011) and Chaves *et al.* (2011) found *inornata* to be sister to all other taxa in the genus. The geographically most proximate and closest-related population, *chlorospila* of Peru, differs by 6.2% in mtDNA (Chaves & Smith 2011: 7, Table 2). Further research into the voice of this population and others in the genus is needed and field work in southern Peru should investigate whether *inornata* is parapatric, sympatric or allopatric with respect to *A. m. chlorospila*, as their ranges abut closely. Because *inornata* was apparently lumped without justification by Peters (1945), it could be argued that the molecular study of Chaves & Smith (2011) together with the data presented here are sufficient to restore it to species rank, as has been proposed for some

other hummingbirds (*cf.* Collar & Salaman 2013, Lozano-Jaramillo *et al.* 2014). The next oldest lineage, *chlorospila* of Peru, also differs in morphology from other populations (Fig. 11) but morphological, vocal and molecular data present a complex situation in northern and central Peru, which necessitates further study.

Discussion

Six options exist to deal with the taxonomy of the Santander–Boyacá population, for those who wish to recognise it as a subspecies: (i) establish a neotype for *sabinae* based on the type of *melanogenys*, placing them in objective synonymy, and describe the Santander–Boyacá population as a subspecies; (ii) establish a neotype for *sabinae* using a modern Santander–Boyacá specimen; (iii) treat *sabinae* as a *nomen dubium* and describe the Santander–Boyacá population as a subspecies; (iv) treat *sabinae* as a *nomen dubium* and retain the status quo; (v) ascertain or clarify the type locality of *sabinae* as the immediate Bogotá region, treat *sabinae* as a subjective junior synonym of *melanogenys* and describe the Santander–Boyacá population as a subspecies; or (vi) ascertain or clarify the type locality of *sabinae* as the range of the Santander–Boyacá population.

In our view, any neotype solution involving *sabinae* is not feasible. It is a requirement for doing so that 'no name-bearing type specimen … is believed to be extant'. There are reasons to believe that MNHN 347 may be a type specimen. An application could be made to the Commission that a neotype to be designated, but we do not propose this yet.

Treating *sabinae* as a *nomen dubium* potentially avoids controversy, but leaves the Santander–Boyacá population unnamed, which does not facilitate communication, the ultimate purpose of taxonomy and nomenclature. A description could easily be reversed, in the event that a new name was subsequently demonstrated to be a junior synonym of *sabinae*, but could also be criticised because it can be argued that *sabinae* is not a *nomen dubium* if MNHN 347 is the type specimen.

Under Art. 76 of the Code (ICZN 1999), the type locality of a name is the 'geographical … place of capture, collection or observation of the name-bearing type'. Recommendation 76A refers to 'ascertaining or clarifying' a type locality. This should be based on (1) data accompanying the original material, (2) collector's notes, itineraries or personal communications (3) the original description of the taxon; and (4) 'as a last resort', localities within the known range of the taxon or from which specimens referred to the taxon have been taken. Although *A. melanogenys* is common in forests and mature second growth near Bogotá, it does not occur in Bogotá itself except as a vagrant (ABO 2000). As a result, the locality specified on the label should not be automatically equated with the city; it was more likely taken somewhere else 'dans la Nouvelle-Grenade'. No collector's notes, information in the original description or data accompanying the original material provides more detail as to the locality. It is therefore usual to adopt the 'last resort' approach under Recommendation 76A with respect to 'Bogotá' or 'Nouvelle-Grenade' specimens of resident species. 'Bogotá' and 'Nouvelle-Grenade' (or 'New Grenada' or 'Colombia') are often used indiscriminately and interchangeably on older specimen labels. Because such specimens are trade specimens, the location is the place of purchase, not necessarily the collection locality. Several such types are now considered to have been collected rather far from Bogotá. For example: (i) that of White-rumped Sirystes *Sirystes albocinereus* was probably collected in Amazonia or at much lower elevations on the east slope of the Andes below Bogotá (Hellmayr 1927, Donegan 2013); (ii) at least one of the original types and the neotype of Yellow-breasted Brush Finch *Atlapetes latinuchus* '*simplex*' were probably taken in Nariño, southernmost Colombia, or northern Ecuador (Donegan & Huertas 2006); and (iii) the type of East Andean Antbird *Drymophila caudata* was probably collected in Santander

(Isler *et al.* 2012) or now-deforested parts of Boyacá (Donegan *et al.* 2012). Most 'Bogotá' specimens of *Adelomyia* are typical of the nominate. However, some show more extensively rufous underparts than dpto. Cundinamarca birds, so are here considered referable to the Santander–Boyacá population (Appendix 3) and others (e.g. AMNH 483486, 'Colombie', formerly of the Boucard collection and others at AMNH) clearly belong to *A. m. cervina*, so were collected in the West or Central Andes.

In light of the above, we therefore tentatively clarify the type locality of *sabinae* as dpto. Santander or north dpto. Boyacá on the west slope of the East Andes, i.e. the range of Clade F of Chaves & Smith (2011: Fig. 1b) and Chaves *et al.* (2011: Fig. 5), and that of subspecies *sabinae* in McMullan & Donegan (2014: 131). The main advantage of using the type locality to resolve taxonomy provisionally is that this can easily be re-evaluated if and when further information becomes available. A disadvantage is the lack of certainty compared to a successful application to ICZN to establish a neotype. We appreciate that some authorities may prefer to treat the Santander–Boyacá population as part of the nominate subspecies.

The core range of the Santander–Boyacá population today is in Serranía de los Yariguíes, where *A. melanogenys* was one of the most abundant species mist-netted: 68 different individuals were trapped at nine localities at 1,350–3,000 m elevation during surveys in 2003–11 (Donegan *et al.* 2010). In the Santurbán massif, west slope of the East Andes in Santander, it was also widespread, being found at 12 localities at 1,250–3,400 m (JEA pers. obs.). The distributional limits of the Santander-Boyacá population to the north and east doubtless coincide with the dry río Suárez / Chicamocha canyon and high elevations of the East Andes. Extensive deforestation has occurred on the west slope of the East Andes in Boyacá, making its southern limit more difficult to define. This population also ranges south at least to Alto de Onzaga, Soatá (Fig. 4C) and Arcabuco, Boyacá (Appendix 3). *A. melanogenys* has not been reported in Serranía de las Quinchas (Stiles *et al.* 1999, Stiles & Bohórquez 2002, Laverde *et al.* 2005, Quevedo *et al.* 2006), but surveyed localities may have been too low in elevation. The extensive ICN series of East Andes *Adelomyia* includes the nominate subspecies from east slope localities in dpto. Boyacá (e.g. Garagoa, Pajarito) and west slope specimens from dpto. Cundinamarca (e.g. Fusagasugá) but not further north.

Further molecular studies are required to definitively resolve the taxonomy and nomenclature of *Adelomyia* in the East Andes of Colombia. Three specimens of the Santander–Boyacá population studied by Chaves & Smith (2011) and Chaves *et al.* (2011) had identical haplotypes and two reportedly showed minor differences, but a discrepancy is evident in the sequences at GenBank. When phylogenetic analyses are replicated, one of the five specimens falls within the *aeneosticta* clade (IAVH 8331, tissue JLPV61 accession no. JF89402) (G. Bravo *in litt.* 2015). This issue perhaps led to $n = 4$ being incorrectly mentioned by Chaves & Smith (2011: Fig. 3). This specimen should be re-sampled. Our Yariguíes series at ICN, MNHN 347 and the types of *A. simplex* and *A. melanogenys* should also be sequenced. If molecular work shows that none of the names *sabinae*, *simplex* or *melanogenys* can be related to the Santander–Boyacá population, then description of the Santander–Boyacá population would be warranted.

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Appendix 1: biometric data from mist-net captures and specimens of Speckled Hummingbirds

Data are presented as follows: mean ± standard deviation (lowest recorded value–highest recorded value) (n = no. of specimens or individuals).

Taxon	Wing-chord (mm)	Tail (mm)	Total culmen from skull (mm)	Body mass (g)
Mist-net captures				
Santander–Boyacá population Yariguíes	55.42 ± 3.19 (49.0–62.0) (n=48)	37.10 ± 3.12 (31.0–42.5) (n=45)	17.92 ± 0.96 (15.9–20.0) (n=46)	4.09 ± 0.48 (3.0–5.1) (n=47)
melanogenys / connectens: Churumbelos, East Andes	54.19 ± 3.54 (47.0–67.0) (n=67)	34.06 ± 2.12 (30.9–37.2) (n=12)	15.63 ± 0.86 (14.2–17.8) (n=16)	4.05 ± 0.38 (3.3–4.8) (n=80)
cervina: Tambito, West Andes	59.40 ± 2.70 (55.0–62.0) (n=5)	/	16.00 ± 1.73 (15.0–18.0) (n=3)	5.4 ± 0.57 (4.7–6.1) (n=4)
Specimens				
Santander–Boyacá population All	51.71 ± 2.98 (47.0–56.0) (n=7)	33.36 ± 2.39 (30.5–37.0) (n=7)	16.57 ± 1.10 (15.0–18.0) (n=7)	3.87 ± 0.49 (3.0–4.5) (n=6)
Santander–Boyacá population Males	52.25 ± 2.99 (49.0–56.0) (n=4)	32.63 ± 2.98 (30.5–37.0) (n=4)	17.25 ± 0.87 (16.0–18.0) (n=4)	3.85 ± 0.62 (3.0–4.5) (n=4)
melanogenys All	50.08 ± 2.72 (46.0–56.0) (n=13)	33.00 ± 1.53 (31.0–36.5) (n=11)	17.65 ± 1.07 (15.0–19.0) (n=13)	3.68 ± 0.52 (3.0–4.9) (n=13)
melanogenys Males	51.86 ± 2.12 (50.0–56.0) (n=7)	33.43 ± 1.59 (32.0–36.5) (n=7)	17.57 ± 1.30 (15.0–19.0) (n=7)	3.70 ± 0.34 (3.0–4.0) (n=7)

Appendix 2: vocal data

For each population, data are presented as follows: mean ± standard deviation (lowest recorded value–highest recorded value) (n = no. of vocalisations analysed). n_{ai}=x in respect of each vocalisation for each population, refers to the assumed no. of individuals sampled.

1. Songs

Taxon	Total song length (seconds)	Max. frequency (kHz)	No. of notes in trill	Length of trill section (seconds)	Speed of trill section (notes/second)
Santander–Boyacá population n_{ai}=13	3.62 ± 2.83 (1.49–13.33) (n=16)	11.39 ± 0.28 (11.03–11.98) (n=18)	12.14 ± 3.57 (7.0–18.0) (n=14)	0.94 ± 0.30 (0.46–1.50) (n=16)	13.89 ± 2.77 (8.71–17.88) (n=14)
melanogenys n_{ai}=11	3.04 ± 0.85 (1.38–4.83) (n=21)	11.20 ± 0.79 (9.69–12.22) (n=21)	7.40 ± 2.74 (2.0–13.0) (n=20)	0.65 ± 0.27 (0.17–1.27) (n=21)	11.90 ± 2.87 (7.08–18.11) (n=20)

Taxon	No. of longer notes	Length of longer notes section (seconds)	Speed of longer notes section (notes/second)
Santander–Boyacá population n_{ai}=13	9.28 ± 8.16 (4.0–40.0) (n=18)	2.50 ± 2.69 (0.92–12.50) (n=18)	4.10 ± 0.86 (2.82–5.46) (n=18)
melanogenys n_{ai}=11	8.43 ± 2.89 (4.0–16.0) (n=21)	2.38 ± 0.81 (0.87–4.05) (n=21)	3.60 ± 0.53 (2.76–4.61) (n=21)

2. Calls

Taxon	Speed (notes/seconds)	Max. frequency of typical note (kHz)	Min. frequency of typical note (kHz)	Bandwidth of typical note (kHz)
Santander–Boyacá population n_{ai}=7	1.56 ± 0.18 (1.26–1.71) (n=7)	10.90 ± 0.45 (10.33–11.51) (n=7)	9.08 ± 0.35 (8.70–9.65) (n=7)	1.82 ± 0.57 (1.33–2.80) (n=7)
melanogenys n_{ai}=3	1.87 ± 0.16 (1.59–1.98) (n=5)	10.70 ± 0.14 (10.56–10.86) (n=5)	9.33 ± 0.16 (9.17–9.56) (n=5)	1.37 ± 0.25 (1.10–1.69) (n=5)

Sound recordings studied

Santander–Boyacá population. Songs. Alto Cantagallos, Serranía de los Yariguíes, San Vicente de Chucurí, dpto. Santander (06°49′N, 73°22′W; 2,400 m) (XC64410, 64412: T. M. Donegan). Reserva Páramo la Floresta, Serranía de los Yariguíes, Zapatoca, dpto. Santander (06°49′N, 73°19′W; 2,800 m) (XC246073–075, 246077–078 and unarchived recordings with original file numbers disc 22 tracks 49–50 and 58–59 and disc 23 track 13: T. M. Donegan). La Aurora, Serranía de los Yariguíes, Galán, dpto. Santander (06°38′N, 73°23′W; 2,700 m) (XC64559: T. M. Donegan). Alto de Onzaga, Soatá, dpto. Boyacá (06°34′N, 72°44′W; 2,500 m) (XC12688: O. Laverde). Calls. RNA Reinita Cielo Azul, Serranía de los Yariguíes, San Vicente de Chucuri, dpto. Santander (06°51′N, 73°23′W; 1,800 m) (XC14023: B. Davis). Rogitama, Reserva Principe de Arcabuco, dpto. Boyacá (05°47′N, 73°26′W; 2,500 m) (XC18358: H. van Oosten). XC246073 (as above). XC264071 (as XC246073). XC64408, 64422 (both, as XC64410). Unarchived recording disc 21 track 93 (as XC264071).

A. m. melanogenys: Songs. Sisavita, Carrizal, Cucutilla, dpto. Norte de Santander (07°26′N, 72°50′W; 2,400 m) (XC117529, 117545: S. Córdoba). Finca Buenos Aires, Vereda Los Alpes, Recetor, dpto. Casanare (05°20′N, 72°46′W; 2,050 m) (XC245571, 245573, 245580, 245604: O. H. Marín Gómez). Finca La Garantía, vereda Brisas del Tonce, Chameza, dpto. Casanare (05°15′N, 72°53′W; 1,500 m) (XC245542: O. H. Marín Gómez). El Secreto, Garagoa, dpto. Boyacá (05°04′N, 73°22′W; 2,000–2,200 m) (XC12340: O. Laverde). Farallones de Medina (or río Gazaunta cuenca alta, Miralindo), Medina, dpto. Cundinamarca (04°35′N, 73°26′W; 2,100 m) (XC94059: O. Cortés; XC117210, 117212, 117213: M. Álvarez Rebolledo). Calls. El Calvario, dpto. Meta (04°22′N, 73°44′W; 2,100 m) (XC96206, 96215, 96241, 96255: O. Cortés). XC89354 (as XC94059).

Appendix 3: specimens attributable to Santander–Boyacá population

ICN, IAvH and MNHN specimens are illustrated in Figs. 1–2, 3 and 8, respectively. Several of the IAvH series are denoted 'A. melanogenys subsp. AMC' on the specimen label. Identification of various specimens

as of indeterminate 'subsp.' had been added to some Santander specimen labels by JEA during 2011 when he was curating the collection. A. M. Cuervo, who wrote 'subsp.' on some other specimen labels together with his initials, has confirmed this denotation was intended to indicate that the specimens are representatives of Chaves & Smith's (2011) Santander–Boyacá clade and that he is not working on a separate publication or description (A. M. Cuervo pers. comm. to J. E. Avendaño 2013).

Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN 35820), adult male, Cerro La Luchata, east slope of Serranía de los Yariguíes, vereda El Alto, Galán, dpto. Santander (06°37′45.1″N, 73°18′53.2″W; 2,100 m), by JEA & A. Masías, on 17 April 2006.

ICN 34816, adult male, vereda Alto Cantagallos, west slope of Serranía de los Yariguíes, San Vicente de Chucurí, dpto. Santander (06°49′N, 73°22′W, 2,400 m), by TMD, E. Briceño (EB) and B. Huertas (BH) and prepared by TMD, on 8 January 2004 (not 2003 as per the label).

ICN 34364, adult male, El Talismán, west slope of Serranía de los Yariguíes, San Vicente de Chucurí, dpto. Santander (06°85′N, 73°22′W, 2,000 m) by TMD, EB & BH and prepared by BH on 6 January 2003.

ICN 36458, male, Finca El Brasil, vereda Retiro Grande, Bucaramanga, dpto. Santander (06°37′34″N, 73°18′53″W, 2,100 m), by JEA on 17 April 2006.

ICN 34987, female, El Mortiño, km 18 vía Pamplona, Floridablanca, dpto. Santander by G. Alarcón-Nieto on 26 June 2004.

IAvH 8331, male, Reserva Cachalú, Encino, dpto. Santander (06°04′26″N, 73°07′45″W, 2,080 m) by J. L. Parra on 28 August 2006.

IAvH 8335, *idem*, 30 August 2006, 2,100 m, unsexed.

IAvH 8336*, *idem*, 2,080 m, unsexed.

IAvH 10293 male, río Pomeca, Arcabuco, dpto. Boyacá (05°48′80″N, 73°28′97″W), by M. Álvarez & C. l. Bohórquez.

IAvH 10562, male, Costilla de Fara, Cuchilla la Vieja, Inspección de Virolín, Charalá, dpto. Santander (06°06′19″N, 73°13′20″W; 1,750 m), by M. Álvarez, A. M. Umaña, S. Sierra & C. Roa in March 1999.

IAvH 13446, female, Estación Experimental y Demostrativa El Rasgón, Piedecuesta, dpto. Santander, by A.M. Umaña, F. Forero & S. Socorro with JEA on 20 September 2004.

IAvH 13463*, *idem*, male, 21 September 2004.

MHN-UIS 1196, unsexed, Reserva del Acueducto La Plazuela, km 28 via a Pamplona, Tona, dpto. Santander by JEA on 1 August 2002.

USNM 372893*, female, above Virolín, Santander, 7,000 ft. by M. A. Carriker on 17 September 1943.

USNM 410760, male, Hacienda Las Vegas, dpto. Santander, 6,000 ft. by M. A. Carriker on 23 August 1949.

USNM 410762*, *idem*, 24 August 1949.

NHMUK: 2002.3.897, 'Colombia, Bogotá', ex Gould collection.

AMNH 483498, 'Bogota', ex Rothschild collection.

MNHN 347, the possible type of *sabinae*, see text.

* = those specimens not distinguishable in lower underparts coloration from other East Andes specimens. Note: given that some specimens are not distinguishable from the nominate population, other 'Bogotá' or 'Colombia' specimens of more ambiguous underparts coloration doubtless also refer to this population.

Appendix 4: morphology of the Santander population
The following is based on ICN 35820. Colours follow Munsell Color (2000), taken by TMD at ICN in June 2012. Crown, dorsal plumage and wing-coverts darkish glittering green (not coded). Flight feathers and alula dusky (10YR 2/1). Uppertail dusky (as above) but tinged greenish. All tail feathers tipped buffy (10YR 7/4), more extensive on outer feathers. Undertail also becomes buffy (10YR 6/4) towards body, appearing more extensively so on outer feathers. Undertail-coverts cream (10YR 7/2.5). Ground colour of flanks warm orange-rufous (near 5YR 6/6) broadly spotted with glittering green tear-shaped spots. Ground colour of throat, mid-belly, supercilium and small post-ocular spot dirty cream (5YR 8/2). Dense spotting on throat, with glittering green tear-shaped dots arranged in six distinct lines, with dots smaller towards bill. Speckling less intense towards breast. Bill from skull to tip 20 mm, or 14.5 mm (tip to feathers), wing-chord 55 mm, tail 36 mm. Label data: mass: 4.0 g; left testis 2.3 × 2.1 mm; right testis 2.9 × 2.3 mm; iris dark brown; bill black; tarsus dark purple, with white soles to feet; no moult noted. Previously mist-netted, ringed and released on 28 June 2005 (recaptured and released later same day and again on 30 June 2005) by TMD, JEA & BH. (ProAves metal hummingbird ring number N80369 on right tarsus.)
There is some variation in the series. Consistent with female plumage of other subspecies, ICN 34987 is paler glittering green on forecrown but otherwise similar to males. IAvH 13463 has a paler throat than other specimens, with less dense streaking and, unlike other Santander–Boyacá specimens, appears to lack such extensive rufous markings on flanks, being indistinguishable from southern East Andes specimens.

The poorly known Mohéli Shearwater *Puffinus* (*persicus*) *temptator* at the Comoro Islands, western Indian Ocean

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SUMMARY.—The results of a pelagic expedition to study Mohéli Shearwater *Puffinus* (*persicus*) *temptator* at sea off the islands of Grande Comore, Mohéli and Anjouan, in the western Indian Ocean, in November 2014, are presented. Variation in the underwing pattern of *temptator* is described for the first time, as are its foraging behaviour and behaviour at sea, providing the first natural history data for this poorly known taxon. In addition, observations of an unidentified, smaller shearwater, are also reported.

Mohéli Shearwater *Puffinus* (*persicus*) *temptator* is known to breed only on Mohéli, in the Comoro Islands, western Indian Ocean (Brooke 2004, Safford & Hawkins 2013). The taxon was described by Louette & Herremans (1985), based on a single specimen now in Tervuren, Belgium, and is among the most enigmatic Indian Ocean seabirds, while its taxonomy remains controversial (Bretagnolle *et al.* 2000, Austin *et al.* 2004). In October 2000, VB visited the Comoros: on Anjouan, he found a tiny colony of a small shearwater, which based on calls and cliff-breeding (*cf.* Bretagnolle *et al.* 2000) was assigned to Tropical Shearwater *P. bailloni*, although none was caught. He also visited the summit of Mohéli, in a successful attempt to relocate the *temptator* colony at night, although none was trapped. Based on this, we estimated the best season to visit the seas around Mohéli to conduct an ocean-based study, and, in November 2014, HS made a pelagic census of *temptator*, with the aim of documenting photographically large numbers of individuals, of all ages and moult stages, to acquire a better understanding of the taxon's characteristics. Large numbers of *temptator* were found, enabling us to describe the taxon's plumage variation, both individual and age-related. In addition, HS discovered the presence of an apparently distinct smaller shearwater, whose identity we discuss. To our knowledge, our pelagic seabird survey is the first of its kind in Comoros, but we hope that our observations will stimulate further research.

The Comoros comprise four main islands—Grande Comore, Mohéli, Anjouan and Mayotte—totalling 2,033 km², which lie halfway between Africa and Madagascar in the northern Mozambique Channel. All four islands are of volcanic origin. The capital, Moroni, is on Grande Comore, which has an active volcano, Mount Karthala. Climate is humid and tropical, with temperatures in the lowlands averaging *c.*28°C in March and 23°C in August. The monsoon lasts from December to April; rainfall peaks in January with on average 420 mm, while October is the driest month, with 85 mm mean rainfall; cyclones are frequent in summer.

Mohéli (211 km²) is the smallest of the main islands and the least populated. The island comprises a plateau at *c.*300 m, and its central ridge reaches 790 m in the west. The valleys are generally fertile and the hillsides covered by dense forests. A shallow oceanic ridge connects Grande Comore and Mohéli, and most of the foraging Mohéli Shearwaters were observed there.

Methods

As *temptator* was described based on its largely dark underwing coloration (Louette & Herremans 1985), we sought to document birds at sea with fully spread wings. In specimens the underwing pattern is not readily appreciated, and the precise pattern can be difficult to evaluate on trapped live birds as the relevant feathers often become disordered. HS used local fishing boats on Grande Comore, Mohéli and Anjouan, with each trip lasting 6–8 hours, reaching max. 25 nautical miles offshore, on five days (4, 5, 8, 9 and 14 November 2014, but on 5th the sea was sufficiently rough that it was necessary to return after *c*.2 hours).

On 5 and 8 November 2014, HS tested some of the same chumming techniques employed while searching for Fiji *Pseudobulweria macgillivrayi* and Mascarene Petrels *P. aterrima* (Shirihai *et al.* 2009, 2014), but the chum was placed in fishing nets and a floater used to keep the offal at the surface. As HS found that Mohéli Shearwaters forage mainly in association with feeding frenzies of sardine-eating seabirds and avoid the chum, he elected to employ fast boats to follow the birds. He searched at sea or chummed at locations close to or along oceanic contour lines, in seas between *c*.60 and 915 m deep. A marine GPS (Garmin Colorado 300) was used to mark positions, travel between locations, and log sightings. Surveys were possible only on days with calm, almost windless conditions as the boats were not suitable for rough seas.

Natural history of Mohéli Shearwater

Colony.—Louette & Herremans (1985) did not provide coordinates of the presumed colony of *temptator* close to the summit of Mohéli, on a forested ridge, but they indicated that the site was near 'Chalet St Antoine II', at *c*.670 m, where a cabin with a meteorological station was sited. In September and November 1983 they heard shearwaters giving a 'tche-reh-tèè, 3–5 times consecutively, *ad nauseam*', mostly at *c*.19.00–20.00 h, occasionally later at night and again before dawn, but were unable to see the birds well in the darkness. Previously, on 23 February 1975, Cheke & Diamond (1986) had heard a shearwater calling in the same area at night. In October 2000 VB again heard birds vocalising near the summit of Mohéli at *c*.12°29'S, 43°67'E. Two other nights spent on the same ridge, but further east (*c*.12°31'S, 43°69'E), were unsuccessful as no shearwaters were heard. Although southern slopes are steeper, the colony seemed to be restricted to north-facing slopes, with most calling heard at *c*.600 m, on hills facing north and north-east, i.e. facing sea areas where the largest numbers of birds were later found (see below). Although the colony's precise extent is unknown, it appeared to be at least 500–750 m linearly, on steep slopes (but not on cliffs).

Numbers at sea.—During five days at sea, 265 Mohéli Shearwaters were recorded: 178 on 4th between Grande Comore and Mohéli and to the north; four on 5th between Grande Comore and Mohéli; 44 on 8th north and north-west of Mohéli; 16 on 9th north of Anjouan and between Mohéli and Anjouan; and 23 on 14th between Grande Comore and Mohéli. Three areas with concentrations of birds were noted, at 12°06'S, 43°26'E; 12°07'S, 43°38'E; and 12°05'S, 43°47'E. Mohéli Shearwaters regularly associated with tuna (Thunnini) shoals, and on 14 November fed with two Blue Whales *Balaenoptera musculus indica*.

Plumage variation.—Of 265 *temptator* counted, 157 could be aged and were scored using five codes relating to the pattern and darkness of the underwing-coverts (Table 1; Figs. 1–7).

Both adults and fledglings show similar variation, but palest birds (scores 1–2) are mostly adults (75%), with the opposite being true for darkest birds (scores 4–5), which are predominantly juveniles (87.5%). This suggests that the taxon is, to some extent, polymorphic with age, a case known only in some albatrosses and giant petrels *Macronectes*

TABLE 1

Scored (1 to 5 levels) underwing patterns of Mohéli Shearwaters *Puffinus* (*persicus*) *temptator* by the degree of dark on the underwing-coverts (see Figs. 1–7).

	Score 1	Score 2	Score 3	Score 4	Score 5	Totals
Adults (aged by moult and wear to the remiges)	30	32	6	4	1	73
Fresh juveniles (presumably fledglings)	6	15	28	24	11	84
Subtotals	36	47	34	28	12	157

Score 1: whitest example (adult; Figs. 1–2). Score 2: greater and fore coverts darker (juvenile; Fig. 3). Score 3: extensively dark but white band complete (adult; Fig. 4). Score 4: almost the darkest with rear greater coverts and fore coverts connected (adult; Fig. 5). Score 5: the darkest underwing with white band very narrow and incomplete (white axillaries and median coverts separated; Figs. 6–7) (both juveniles).

among Procellariiformes (Bretagnolle 1993), although young shearwaters of some species are darker/blacker, especially dorsally, vs. adults, e.g. *P. bailloni* (Bretagnolle & Attié 1996) and Yelkouan Shearwater *P. yelkouan* (HS pers. obs.), while plumage variation in *P. subalaris* (Galápagos Islands; HS pers. obs.) includes some birds with underwing patterns as blackish as in *temptator*, but relating age to this variation in *subalaris* remains to be established.

Breeding.—Moult stage is indicative of life-cycle stage in petrels, especially if age can be estimated. Most adults observed (>80%) or photographed showed signs of active moult in the (mostly inner) remiges and upperwing-coverts. These were probably either non-breeders or post-breeders (remiges are usually replaced in the non-breeding season in shearwaters). As non-breeding activity peaks during early chick-rearing, and because recently fledged birds were observed, we suggest that the Mohéli colony was either at the very late breeding stage, or nesting spans late winter to early summer, as in *P. bailloni* on Réunion (Bretagnolle *et al.* 2000) and *P. b. nicolae* on Seychelles (L. Calabrese, G. Rocamora & VB unpubl.).

Foraging behaviour.—Mohéli Shearwaters forage primarily within mixed-species feeding frenzies, mainly involving Sooty Terns *Onychoprion fuscatus* (up to 20 in a single aggregation) and Brown Noddies *Anous stolidus* (up to 230), and, frequently, Masked Boobies *Sula dactylatra* (up to three) and Lesser Frigatebirds *Fregata ariel* (up to five). In addition, HS also identified several Black-naped Terns *Sterna sumatrana* in these feeding aggregations, with 23 in total. Most of the sizeable concentrations numbered several Mohéli Shearwaters. For example, on 4 November 2014, all nine feeding frenzies included 4–33 shearwaters. First to locate shoals of fish are Sooty Terns and, as they start to dive, Brown Noddies appear with the shearwaters, the latter diving below the

Figure 1. Fresh adult Mohéli Shearwater *Puffinus* (*persicus*) *temptator*, with wing score 1, at end of post-nuptial moult (much of body, wing and tail replaced, but several unmoulted inner rectrices), off Mohéli, Comoros, November 2014 (Tubenoses Project & Extreme Gadfly Petrel Expeditions / Hadoram Shirihai)

Figures 2–7. Mohéli Shearwater *Puffinus* (*persicus*) *temptator*, off Mohéli, Comoros, November 2014, showing variation in darkness of underwing-coverts, as scored in this study (see Table 1); the upper- and middle-left (Figs. 2 and 4) and middle-right birds (Fig. 5) are adults during post-nuptial moult of the remiges, while the rest are juveniles (Tubenoses Project & Extreme Gadfly Petrel Expeditions / Hadoram Shirihai)

Figures 8–9. Mohéli Shearwater *Puffinus* (*persicus*) *temptator*, off Mohéli, Comoros, November 2014, with adult on left (recently moulted inner primaries) and a newly fledged juvenile on right, which has a more delicate greyish bill, blacker upperparts with a more sharply delimited cap, but less marked breast-sides; this taxon often appears to have a dark mask around the eye, especially in adults (Tubenoses Project & Extreme Gadfly Petrel Expeditions / Hadoram Shirihai)

surface, then boobies join in, while frigatebirds attack some of the other seabirds. As the flock disperses (or follows the terns), some of the longer/deeper diving shearwaters emerge on the surface, and take off. The primary driver of these feeding frenzies is the tuna and other large-fish predators that attack the sardine shoals, with the location and depth of these aggregations changing daily. Mohéli Shearwaters occurred in such aggregations off all of the surveyed islands, but (at least on 4 November) most were found over and at the edge of the shallow oceanic ridge connecting Grande Comore and Mohéli (12°07S, 43°38E), where shearwaters were observed to forage in association with two Blue Whales around sardine shoals at the north edge of the oceanic ridge (12°04'S, 43°38'E). Several shearwaters were simultaneously observed diving alongside a whale's rostrum, escaping just as the whale closed its mouth.

Taxonomic relationships.—Taxon *temptator* was suggested to be fairly close (if not identical in plumage) to *P. persicus* of the Arabian Sea, which taxon is now frequently treated specifically (e.g., by Onley & Scofield 2007), rather than as a subspecies of *P. lherminieri*. Its measurements (comparison between the type and specimens in Tring and Washington DC: Louette & Herremans 1985; pers. obs) agree in size (note USNM 571356, treated in Louette & Herremans 1985 as *persicus*, is probably a *bailloni*; VB pers. obs.), while molecularly *temptator* and *persicus* are very close (Austin *et al.* 2004). Comparison of many photographs of the two taxa reveals the same variation in the underwing-coverts, similar breast-side patches, degree of dark on the undertail-coverts and vent, and same overall pattern. Mohéli Shearwaters often has the impression of a dark mask around the eye, especially in adults, which is shared by *persicus*, but *temptator* almost always lacks the almost invariable, small but distinctive whitish patch in front or above the eye of *persicus*; *temptator* also seems to have bluer/greyer, less pinkish/flesh-toned bare parts, most notably the tarsi and webs.

Population and conservation.—As no burrows have been found, the population size of Mohéli Shearwater can only be guessed. Brooke (2004) suggested a total population of <500 individuals. In October 2000, VB found that colony extended over at least a few hectares, on several high ridges on the north slope of central Mohéli, much of which is inaccessible due to the lack of trails. Two nights elsewhere in the hills of central and southern Mohéli did not reveal any other colonies that year. In the colony, peak calling rate (just after nightfall) was rather high (*c.*30 calls/minute), suggesting that several hundred pairs were breeding (based on comparison with call rates at known-size colonies of *P. bailloni* on Réunion:

Bretagnolle *et al.* 2000). Equally, that nearly 300 individuals were observed during a few days at sea indicates a similar-sized breeding population at least. The altitude/vegetation where shearwaters have been heard was not inhabited or exploited by humans (at least in 2000), but the island's north slope is more impacted (and the forest's lower elevation limit is higher) than in the south. Cleared land lay just a few hundred metres from the colony in places.

Unidentified small shearwater off the Comoros

During November 2014, HS also noted several shearwaters that appeared different in size, jizz and behaviour, with different coloration patterns (Figs. 10–13). These seemed smaller and slighter with a smaller and rounder head shape, and proportionately broad and short bill. They also behaved quite differently, nearly always feeding alone, only rarely joining the mixed-species feeding frenzies of other seabirds including Mohéli Shearwaters, enabling direct comparison. In total 14 such birds were observed, on 4 (nine) and 8 November (five). Initially, HS considered the possibility of not yet fully grown fledgling Mohéli Shearwaters, as they appeared blacker above and very fresh. However, with closer views and photographs, it was clear that these birds were fresh adults completing moult of their remiges.

At least two other taxa of Tropical Shearwater may occur in these waters: *bailloni* of Réunion Island (and formerly Mauritius, as well as possibly Europa in the Mozambique Channel), and *nicolae* (including *colstoni* of Aldabra) on Seychelles (Figs. 14–15). However, the birds observed in November 2014 had dark undertail-coverts and some dark on the underwing-coverts, eliminating *bailloni*, although this taxon had been thought to be present (based on calls) on Anjouan (VB pers. obs.). Furthermore, their flight, being more elastic like Little Shearwaters *Puffinus assimilis*, with clearly bluer bills and paler ear-coverts (sometimes with an indistinct whitish supercilium), suggest they were not *nicolae*. Interestingly, they displayed quite strong variation from pale (Fig. 10) to darker underwing-coverts (Figs. 11–13), though not as extreme as the variation in *temptator*.

Concluding remarks

During November 2014 we successfully located Mohéli Shearwater, and for the first time documented its plumage photographically. We also collected basic data concerning its range and numbers at sea, as well as its behaviour, providing the first natural history information for this poorly known taxon.

Mohéli hosts the only known breeding colony of Mohéli Shearwater. Other seabirds there include a large roost of frigatebirds on the southern islets (several thousand birds; VB pers. obs.), while a rocky islet off the east coast supports breeding boobies and terns. The only other petrel breeding on the Comoros is a small shearwater found on Anjouan by VB, initially considered to be *bailloni* based on vocalisations and breeding habitat, but equally possibly could represent the unidentified small shearwater HS observed at sea in 2014. Cliff-breeding is known for *bailloni*, but was unknown for *nicolae* until recently, when very small numbers were rediscovered on Mahé, Seychelles, on the island's highest peaks (G. Rocamora pers. comm.). Therefore, cliff-breeding does not eliminate *nicolae* as the taxon on Anjouan, as originally thought. The smaller shearwaters photographed by HS represent either an extreme variation (of certain age/sex classes) of *temptator*, or an undescribed taxon superficially resembling *nicolae* and probably the same taxon as breeds on Anjouan. The combination of Little Shearwater-like characters (small size, squat jizz, pale supercilium) and predominately bluish and short, broad bill makes these birds distinctive. Unlike

Legend to figures on facing page

Figures 10–13. Unidentified adult/immature small *Puffinus*, off Mohéli, Comoros, November 2014, two different individuals, with a paler underwing (top left), and a darker example (other images) (Tubenoses Project & Extreme Gadfly Petrel Expeditions / Hadoram Shirihai)

Figures 14–15. Fresh adult Tropical Shearwaters *Puffinus b. bailloni*, Réunion, December 2012 (left), and *P. b. nicolae*, Seychelles, November 2014; white undertail-coverts and extensive, whiter underwing-coverts in former, whereas these are brown and marbled dark, respectively, in latter (Tubenoses Project & Extreme Gadfly Petrel Expeditions / Hadoram Shirihai)

nicolae (including *colstoni*), the breast-side patches are weakly developed in size, colour and boldness, but are to some extent more like *bailloni*. The geographically closest breeding taxon is *colstoni* on Aldabra, but, at least in adults, this taxon is rather large (intermediate between *bailloni* and *nicolae*) with a characteristically thick bill (Shirihai & Christie 1996, Bretagnolle *et al.* 2000), making it unlikely that the unidentified Comoros shearwaters are *colstoni*. Nevertheless, most available morphometric data for these *Puffinus* are of adults and fledglings, whereas immature non-breeders are very poorly known, so we cannot eliminate that these unidentified shearwaters represent hitherto unknown age-related variation. Until such birds are captured for biometrics and DNA, their identity must remain unknown.

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New avian observations from south-western Ethiopia, with a review of overlooked literature and altitudinal limits

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SUMMARY.—Observations are discussed that augment or amend data presented in the standard avifauna of Ethiopia (Ash & Atkins 2009) for the south-western corner of the country. Two species are detailed for the first time (Violet Wood-hoopoe *Phoeniculus damarensis*, Purple Indigobird *Vidua purpurascens*); the second certain localities for Barka Indigobird *V. larvaticola* and Wilson's Indigobird *V. wilsoni* are reported; and the specific status of Little Rush Warbler *Bradypterus baboecala* in Ethiopia is established. Other records include those relating to species previously unreported in October, and altitudinal limits that differ substantially from those presented by Ash & Atkins. We also detail a number of previously published records that were not reflected in the maps in Ash & Atkins. In Appendix 1 we list *c.*200 species / square records that are additional to those mapped by Ash & Atkins.

We spent a month in the field in south-western Ethiopia, between 10 October and 7 November 2014, at a time of year for which Ash & Atkins (2009) surprisingly often lacked observations. Thus field records are presented that augment or amend the work of Ash & Atkins. We also detail (Appendix 1) species / square records additional to those in their maps. Those authors do not quantify the thoroughness of their atlas coverage, so it is impossible to see where further field work is required; but among more than 200 additions there are in excess of 20 from the Uajo River square, between Sodo and Lake Abaya (0637D) alone. Some of our additions may reflect inaccurate plotting in Ash & Atkins' atlas: for example, in their gazetteer (p. 423) they gave coordinates for Turmi as 05°02′N, whereas they are correctly 04°58′N—thus the town and lodge of that name are in square 0436C and the Kaske River crossing in 0436D. Relevant literature records overlooked by Ash & Atkins are also listed. In addition, N. Redman (*in litt.* 2014) and N. Borrow (*in litt.* 2014) generously provided their own observations relevant to this paper. In the case of N. Borrow, his records had been submitted to J. Ash prior to the publication of Ash & Atkins, but most were unfortunately ignored therein. We also comment on some records in the literature relating to the areas we visited (Francis & Shirihai 1999, Tilahun *et al.* 2001, Spottiswoode *et al.* 2010) which we believe are in error or require confirmation.

Ash & Atkins numbered their atlas map squares independently of the more practical method of relating them to degrees of latitude and longitude (in this case squares of 30 × 30 minutes). In this paper we relate squares to their central point, thus square 0734B (Ash & Atkins' plot 79d, see their p. 63) is centred on 07°15′N, 34°45′E. Unless otherwise stated all observations are our own and relate to October–November 2014. Some observations were made in the company of M. N. Gabremichael and S. Rooke, and these are indicated as 'FD-L *et al.*'. Our itinerary included the Gibé escarpment, Sodo, Arba Minch (Nechisar National Park), south to Turmi and Murle (Omo River, Lake Dipa), north to Menagesha forest and Debre Libanos. This was followed by a circuit including the Jemma Valley, Rift Valley lakes, Bale Mountains National Park, Negele, Dawa River and Yabello to Mega. Appendix 2 is a gazetteer of all localities mentioned. Scientific names are those of Dickinson & Remsen (2013) and Dickinson & Christidis (2014), except where stated.

Results

BLACK-NECKED GREBE *Podiceps nigricollis*
One at Lake Dipa on 17 October and at least six on Lake Chamo (Nechisar National Park) on 13 October represent southern extensions of the range as mapped in Ash & Atkins, although the species had been reported from Nechisar by Safford *et al.* (1993).

EURASIAN SPOONBILL *Platalea leucorodia*
Ash & Atkins gave 27 October as the earliest date in autumn for Ethiopia; we saw an immature at Lake Dipa on 17 October (identified by its grey, not yellow, bill and lack of red on the face, thereby excluding African Spoonbill *P. alba*).

RÜPPELL'S GRIFFON *Gyps rueppelli*
Occurrence of the race *erlangeri* in north-east Ethiopia was considered likely by Ash & Atkins; Salvadori (1908) included Shoa in its range, and its type locality has been considered restricted to Shoa region, Ethiopia (e.g. Sclater 1924: 48).

OVAMBO SPARROWHAWK *Accipiter ovampensis*
We saw one on 14 October south of Turmi (square 0436D, 700 m) and one 16 October between Turmi and Murle (0536A, 580 m); Ash & Atkins plotted the latter square as requiring confirmation. The few previous records are for July and November–March, and above 1,270 m.

SOOTY FALCON *Falco concolor*
RJD identified a first-year bird that he observed closely, catching flying insects over Nechisar Plain, on 13 October. Ash & Atkins accepted just four records in Ethiopia, 28 October–30 January, but with further experience J. D. Atkins (*in litt.* 2015) is certain of one he saw in Awash National Park in October. N. Borrow (*in litt.* 2014) reported a juvenile in the Jemma Valley on 9–10 October 2000 and saw an adult at Yabello on 26 October 2004. October birds are presumably on passage to their non-breeding quarters in Madagascar and south-eastern Africa, as revealed by an adult satellite-tracked through eastern Ethiopia in early November, en route from the United Arab Emirates (Javed *et al.* 2012).

HARLEQUIN QUAIL *Coturnix delegorguei*
Two males were flushed together in grassland in Awash National Park (0940A), on 7 November (FD-L *et al.*). In the same area, N. Borrow (*in litt.* 2014) had many records of up to eight individuals between 13 October and 28 December (1994–2012), while two were seen there on 16 November 2013 (N. Redman *in litt.* 2014). Ash & Atkins reported records only for the period 10 February–17 August.

LITTLE BROWN BUSTARD *Heterotetrax humilis*
Listed for Mago National Park and Yabello Sanctuary by Tilahun *et al.* (1996, 2001), but these reports were clearly in error this far west and were not mentioned by Ash & Atkins.

WATER THICK-KNEE *Burhinus vermiculatus*
Reported from the road between Melka Ghebdu and Awash (*c.*09°13′N, 40°00′E) by Shirihai & Francis (1999), but as remarked by Spottiswoode *et al.* (2010) this is considerably to the north of other records in Ethiopia (to 06°N). It is visually difficult to separate from the widespread Senegal Thick-knee *B. senegalensis*, and presumably for that reason the record was not accepted by Ash & Atkins.

RAMERON PIGEON *Columba arquatrix*
Ash & Atkins reported records for all months except September and October. One was in desultory song in Menagesha forest on 20 October. In addition N. Borrow (*in litt*. 2014) recorded a few in October in five different years (1998–2006), in the Bale Mountains, at Wondo Genet and at Wadera.

LEVAILLANT'S CUCKOO *Clamator levaillantii*
Ash & Atkins knew of no record for October, and only two between 27 November and 23 March. However, we saw and heard birds on 11 October on the Gibé escarpment and daily 29–31 October in the Negele square (0539B). N. Borrow (*in litt*. 2014) had records for October (four), November (three), February (one) and March (one), in 1995–2012.

RED-CHESTED CUCKOO *Cuculus solitarius*
It would seem there were no records for September–October (Ash & Atkins), but on 16–17 October a bird was singing by the Omo River at Murle, and we saw and heard one at nearby Lake Dipa. A Red-capped Robin Chat *Cossypha natalensis* imitated this cuckoo in Nechisar National Park (0537D), on 13 October.

YELLOWBILL *Ceuthmochares aereus*
Ash & Atkins accepted only five records that they considered certainly identified, from three localities (Nechisar National Park and surroundings). We heard its vocalisations (familiar to us from eastern Africa) on 12–13 October in the west of Nechisar National Park, but we did not encounter it in the Omo Valley. Ash & Atkins were uncertain as to the subspecies in Ethiopia, but based on vocalisations it is clearly *australis*. Of many uncertain localities in Ash & Atkins, Bishangari has since been confirmed (Spottiswoode *et al*. 2010; M. N. Gabremichael pers. comm.), and J. D. Atkins (*in litt*. 2015) considers that his records from Gore, Metu and Tepi should now be accepted too.

DONALDSON SMITH'S NIGHTJAR *Caprimulgus donaldsoni*
The lack of records in May and August–October, remarked on by Ash & Atkins, probably reflects insufficient field work. On 31 October we photographed one in woodland near Negele (0539B), and several were in song at Borana Lodge, Yabello, on 1 November (FD-L *et al*.).

BLUE-BREASTED KINGFISHER *Halcyon malimbica*
Listed from Mago National Park ('reputedly', Spottiswoode *et al*. 2010) and Omo National Park (Tilahun *et al*. 2001), but we did not find this vocal bird on the Omo, and nor did J. D. Atkins (*in litt*. 2014), during a week in July–August 1996 or M. N. Gabremichael (pers. comm.), thus it was not included by Ash & Atkins.

VIOLET WOOD-HOOPOE *Phoeniculus damarensis*
We found this species in two areas: at Murle, Omo River, where we had very good views of one on 16 October, and a large group at nearby Lake Dipa, on 17 October, with a pair (of which a poor photograph was obtained, Fig. 1) on the 'Little' Kaske River near Turmi, on 18 October. All birds clearly had a strong violet (not greenish) gloss, red bill and legs, and the voice sounded drier than that of Green Wood-hoopoe *P. purpureus*, which we know very well from elsewhere.

Ash & Atkins (2009: 222, 375) stated that the few claims of Violet Wood-hoopoe in Ethiopia (which they treated as a species distinct from *P. purpureus*, under the name *P. d. damarensis*, clearly a *lapsus* for *P. d. granti*) required confirmation. J. D. Atkins (*in litt*. 2014) has stated that he observed what he believed to be Violet Wood-hoopoe on three

occasions in large riverine trees near Lake Dipa in August 1996. Putative observations by the late J. Ash from the same general area of the lower Omo Valley were discussed by Ash & Atkins (2009: 375). Those authors were mistaken to suggest that Peters (1945: 251) cited Neumann (1903) as the source of records he listed from southern Ethiopia (Omo River, Lakes Stephanie and Rudolf), as Peters gave no reference for his statement and Neumann did not mention these localities. In fact, it was Zaphiro who collected two *Phoeniculus* in the Omo region—specimens in NHMUK (formerly BMNH) at Tring, examined by D. A. Turner (*in litt.* 2013). Although Ogilvie-Grant (1913) published on the passerines in that collection, the non-passerines were never documented in print. Zaphiro's birds were from the Zoula River, Uba, 12 July 1905; they are clearly not Black-billed Wood-hoopoes *P. somaliensis* (D. A. Turner *in litt.* 2013) and for the present we treat them as *P. damarensis granti*. This species has also been listed, without documentation, from Omo and Mago National Parks (Tilahun *et al.* 2001, Spottiswoode *et al.* 2010).

The plots in Ash & Atkins of *P. purpureus* range from *c*.11°15′N, 35°15′E south to *c*.07°15′N, 34°45′E (neither locality named). They also plotted eight records of *P. purpureus* which they considered required confirmation, and added that 'scattered birds may reach as far as 38°E'. In fact, Neumann (1905: 194) reported a specimen attributed to *P. purpureus niloticus*, with coral-red bill and legs, from Aveve, Kollu Province, and it is clear from his itinerary (Neumann 1904: 322) that this would have been in square 0938A.

Some authorities have suggested sympatry between various of these three species, but we believe this is unlikely to be the case and that further investigation is required. Two such claims were repeated by C. H. Fry *in* Snow (1978): one was based on the claim by Granvik (1934: 37–38) to have collected both *P. purpureus* (race *marwitzi*) and nominate *P. s. somaliensis* at Kolosia (or Kolothia), Turkana, Kenya, but Granvik made it clear that his specimen of *P. somaliensis* was immature, and the possibility of it being *P. purpureus* was not convincingly rejected. Similarly, Oberholser (1945: 87–88) reported specimens from Archer's Post, Kenya, of both *P. purpureus marwitzi* and *P. (damarensis) granti*. Zimmerman *et al.* (1996) considered that such claims required confirmation.

Concerning the distribution of *P. somaliensis*, we found it only as far west in the south as Yabello, and it is known from Nechisar National Park (Safford *et al.* 1993). J. D. Atkins (*in litt.* 2014) concurs that records of *P. somaliensis* in South Omo should be questioned.

VON DER DECKEN'S HORNBILL *Tockus deckeni* / JACKSON'S HORNBILL *T. jacksoni*

Treated as separate species by Ash & Atkins among others, but as conspecific by Dickinson & Remsen (2013) and Turner & Pearson (2014). An adult male observed closely by RJD on 15 October near the Kaske River (0436D, thus within the range of birds attributed to *T. jacksoni* as well as *T. deckeni*) had some obvious pale flecks on the wing-coverts and mantle, suggestive of possible hybridisation.

SCALY-THROATED HONEYGUIDE *Indicator variegatus*

The altitudinal range given by Ash & Atkins of 1,280–3,030 m does not appear to take into account records they mapped from the south-west (lower Omo), surely at a lower altitude (although they gave no details). We encountered it only at Bishangari, Lake Langano, a well-known site (N. Redman *in litt.* 2014), where a male was at its song perch at midday on 26 October (FD-L *et al.*).
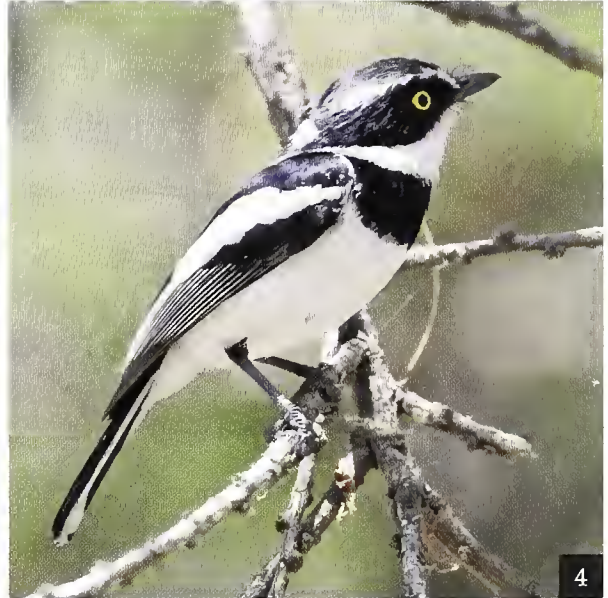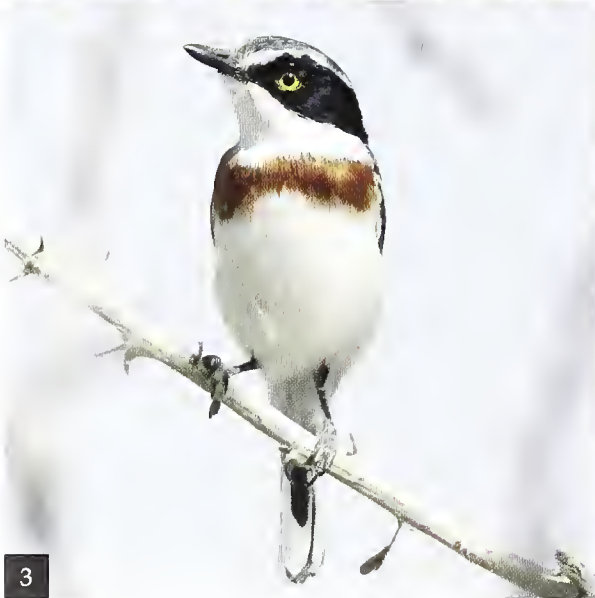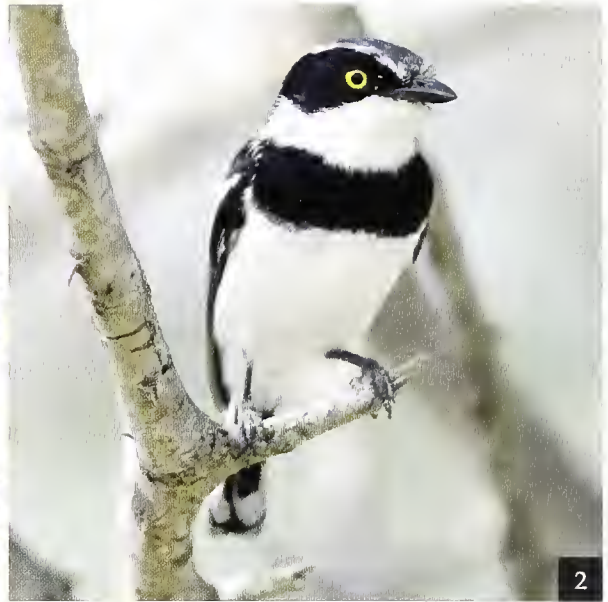
Figure 1. Violet Wood-hoopoe *Phoeniculus damarensis*, Turmi, Ethiopia, October 2014 (R. J. Dowsett)

Figure 2. Male Grey-headed Batis *Batis orientalis*, Lake Langano, Ethiopia, February 2014 (© Dick Forsman)

Figure 3. Female Grey-headed Batis *Batis orientalis*, Lake Langano, Ethiopia, February 2012 (© Dick Forsman)

Figure 4. Male Western Black-headed Batis *Batis erlangeri*, Awash National Park, Ethiopia, January 2010 (© Dick Forsman)

Figure 5. Female Western Black-headed Batis *Batis erlangeri*, Awash National Park, Ethiopia, November 2011 (© Dick Forsman)

PINK-BREASTED LARK *Calendulauda poecilosterna*
Ash & Atkins apparently knew of no records in July–December, but several were singing in dry bush between Turmi and Murle on 16 October. J. D. Atkins (*in litt.* 2015) had in fact recorded several in dry bush in August 1996, also between Turmi and Murle.

WHITE-TAILED SWALLOW *Hirundo megaensis*
The northernmost record of this very local endemic was given as 05°12'N, 38°13'E by Ash & Atkins, although they mapped this as in square 0538C, thus north of 05°30'N. Mellanby *et al.* (2008) found birds north to 05°08'N, 38°17'E in this sector, and further east Gabremichael *et al.* (2009) reported sightings around the Liben Plain (*c.*05°15'N, 39°46'E). The northernmost plot in Ash & Atkins was misplaced (J. D. Atkins *in litt.* 2015).

COMMON REDSTART *Phoenicurus phoenicurus*
The race *samamisicus* is reportedly absent west of 38°E (Ash & Atkins), but a male was well seen on the Gibé escarpment on 11 October and M. Mills (*in litt.* 2015) saw a male there in April 2014.

SNOWY-CROWNED ROBIN CHAT *Cossypha niveicapilla*
Several were singing in thickets at Lake Dipa on 17 October, an area in which there were also White-crowned Robin Chats *C. albicapillus*. This represents a southward extension of the known range in Ethiopia, from atlas square 0735A, although the species was listed without details from Mago National Park (Tilahun *et al.* 2001). Spottiswoode *et al.* (2010) also mentioned it from riparian thicket on the Gibé (= Omo) River in 0837B, an easterly extension of the known range. Ours is the first report for September–October (Ash & Atkins), although this is surely the result of insufficient field work during those months. For both species, Lake Dipa (at 400 m) lowers the known altitudinal limit (*cf.* Ash & Atkins), in the case of Snowy-crowned Robin Chat considerably so.

WHITE-BROWED ROBIN CHAT *Cossypha heuglini*
Ash & Atkins did not detail the north-eastern limit of its range, which is Lake Langano (0738D): several were seen and heard in bush below the cliff at Simbo Lodge, on 3–4 November (FD-L *et al.*), and it is also known from Bishangari (N. Redman *in litt.* 2014).

LITTLE RUSH WARBLER *Bradypterus baboecala*
One was in song in the Awash Swamp at Bilen Lodge, on 6 November (FD-L *et al.*), a new locality for this sparsely distributed bird, but it had been heard there once before, by N. Borrow (*in litt.* 2014) on 10 October 2006. Its voice was similar to the low-pitched vocalisations of southern African populations, although it did not respond to playback of a voice recorded in South Africa (on Gibbon 1991). The species' low-pitched song was sound-recorded at Lake Awassa, where birds did react to playback of a South African recording (M. Mills *in litt.* 2015). These observations confirm those of Benson (1948: 66), who remarked on the fact that vocalisations from Ethiopia and southern Africa were strikingly different from the high-pitched songs of populations centred on west-central Kenya. Molecular analyses confirm the specific distinction between these two groups (Alström *et al.* 2011), for which priority insists the names be *B. baboecala* (type locality South Africa) and *B. centralis* (type locality Rwanda). Most Ethiopian birds are *B. b. abyssinicus*, with *B. b. sudanensis* reportedly the form in the Gambela area (Ash & Atkins).

ORPHEAN WARBLER *Sylvia hortensis*
Although specimens were reported from Gamo, Lake Abaya (0637B) and Gibé (Gibbe) River, Jimma (0837A) by Ogilvie-Grant (1913: 612), he called them in fact the 'Garden-

Warbler', this being the scientific name widely applied then to what is now *S. borin*. Ash & Atkins made no reference to these, but correctly omitted them.

GREY-HEADED BATIS *Batis orientalis* / **WESTERN BLACK-HEADED BATIS** *B. (minor) erlangeri*

We would follow Louette (2005) in granting specific status to *B. erlangeri*. Because Ash & Atkins admitted the difficulty that is often attached to separation of this species from *B. orientalis*, we paid particular attention to the problem. The distinctive vocalisations provide the best means of field identification. We identified *B. erlangeri* in the following areas: Agere Maryam (0538C), Negele (0539B), Sodo and Uajo River (0637D), Awassa (0738A), Bishangari (0738D), Simbo Lodge, Lake Langano (0738D) and Gibé (0837B). It was absent from the drier woodlands in which we found *B. orientalis*, namely the road from Negele to the Genale River (0539B), between Yabello and Mega (0438A, C), Bilen Lodge and Awash National Park (0940A).

Confusion is possible in the field (*cf*. Figs. 2–5) and even specimens can be misidentified. We believe it remains to be proven that the broad range of overlap mapped by Ash & Atkins is indeed correct, despite those authors' optimism, and J. D. Atkins (*in litt*. 2015) now agrees. In particular, N. Borrow (*in litt*. 2014) and S. Rooke (pers. comm.) believe that all records of *B. orientalis* from the highlands are erroneous (we suggest it may not occur above 1,400 m).

BLACK-BELLIED SUNBIRD *Cinnyris nectarinioides*

Listed from Mago National Park by Tilahun *et al*. (2001), but this is a long way from its range in south-east Ethiopia and it was not mapped by Ash & Atkins as considered erroneous (J. D. Atkins *in litt*. 2015). Listed from Yabello by Spottiswoode *et al*. (2010), but the species was not found in that region by Benson (1946), and the western limit confirmed to date is the Dawa River (as mapped by Ash & Atkins). Uncommon there, but one seen on 1 November (FD-L *et al*.).

COPPER SUNBIRD *Cinnyris cupreus*

A male in breeding plumage at Lomi stream, Jemma Valley (0938D, 1,510 m), on 24 October, in which area the species was also reported by N. Borrow (*in litt*. 2014) and S. Rooke (pers. comm.). These confirm the Jemma Valley as the species' easternmost limit, Ash & Atkins having plotted an unconfirmed record in this square, without explanation.

YELLOW WHITE-EYE *Zosterops senegalensis*

Ash & Atkins plotted records for squares 0437D and 0438C, but these are in error, being based on specimens of the race *australoabyssinicus* collected near Yabello and Arero (Benson 1946: 454), a form now known to belong to Abyssinian White-eye *Z. abyssinicus* (R. E. Moreau *in* Paynter 1967: 327). However, FD-L saw *Z. senegalensis* (with bright yellow underparts, the local race *omoensis* of *Z. abyssinicus* having a grey belly) in woodland near Murle (590 m), *c*.05°08'N, 36°13'E, on 16 October, an extension to the south-east.

NORTHERN PUFFBACK *Dryoscopus gambensis*

Ash & Atkins gave the altitudinal range as 480–1,880 m (once at 2,576 m), whereas we found it to be common in Menagesha forest at 2,450–2,600 m, on 20–21 October.

THREE-STREAKED TCHAGRA *Tchagra jamesi*

A pair and a single were observed displaying to each other in thornbush at Awash National Park, on 7 November (FD-L *et al*.); square 0840C is significantly further north than previously recorded (0740D in Ash & Atkins).

STRESEMANN'S BUSH CROW *Zavattariornis stresemanni*
Mellanby *et al.* (2008) found it north to nearly 05°08'N, 38°18'E, i.e. 22 km north of Yabello, a known area (N. Redman *in litt.* 2014). It was reported by Ash & Atkins north to an un-named locality 32 km north of Yabello (their square 109c, which they mistakenly plotted as 109d). We saw it no further north than 05°05'N, 38°16'E (one on 3 November, FD-L *et al.*), i.e. *c.*15 km north of Yabello.

LESSER BLUE-EARED STARLING *Lamprotornis chloropterus*
Clearly Greater Blue-eared Starling *L. chalybaeus* is much more widespread than this species, as shown by Ash & Atkins, *contra* Francis & Shirihai (1999). We found *chloropterus* at just four localities, and *chalybaeus* in well over 25.

MAGPIE STARLING *Speculipastor bicolor*
Ash & Atkins had records for every month except October and November. We found several pairs (at least eight birds) a few km before Murle and others at Murle, on 16–17 October: they were calling and occasionally chasing each other, possibly signs of early breeding activity. In addition, N. Redman (*in litt.* 2014) saw a pair on the Soda Plain on 27 November 2011, and N. Borrow (*in litt.* 2014) two in that area on 26 November 2012.

YELLOW-BACKED (BLACK-HEADED) WEAVER *Ploceus melanocephalus*
Francis & Shirihai (1999) reported this species from the Dawa River on 23 September 1997 (repeated by Spottiswoode *et al.* 2010), at a locality where Juba Weaver *P. dichrocephalus* is known. Although they realised this was unexpected (they did not find Juba Weaver), we consider the record unlikely and in need of confirmation. It was not mapped by Ash & Atkins. Juba Weaver is quite numerous and frequently seen in the region (e.g. 31 October and 1 November, FD-L *et al.*), but the nearest confirmed records of *P. melanocephalus* are of the race *fischeri* from the Imatongs in South Sudan (Nikolaus 1989), more than 500 km to the west.

BLACK-RUMPED WAXBILL *Estrilda troglodytes*
Records from Mago National Park and the Jemma Valley (Tilahun *et al.* 2001) are undocumented and unlikely to be correct; they were not accepted by Ash & Atkins (J. D. Atkins *in litt.* 2014). The nearest confirmed records are in the extreme west, from the Gambela area (Ash & Atkins).

VILLAGE INDIGOBIRD *Vidua chalybeata*
Several (their red legs well seen) with their known host, Red-billed Firefinch *Lagonosticta senegala*, on the Genale River, 25 km north-east of Negele (0539D), on 31 October (FD-L *et al.*) confirm this species' presence in the Negele area, *cf.* 'unconfirmed' records in Ash & Atkins. At present, this is the south-eastern limit in Ethiopia.

PURPLE (DUSKY) INDIGOBIRD *Vidua purpurascens*
On 19 October 2014 we found a male *Vidua* in breeding dress and in song, accompanied by a Jameson's Firefinch *Lagonosticta rhodopareia*, perched in the same small tree. This was in thornbush just north of the road crossing on the Uajo River, between Sodo and Lake Abaya. The brief snatches of song did not include mimicry and as plumage differences in indigobirds (other than Village) cannot be used for species separation in the field its identity is based tentatively on its close association with the known host. Jameson's Firefinch was identified on both visits to the area, south and north of the Uajo River—a pair on 12 October (calling, the typical trill), and a male (also calling) on 19 October. It was apparently the only firefinch present. Surprisingly no nest parasite has hitherto been reported in Ethiopia for

Figure 6. Male Wilson's Indigobird *Vidua wilsoni*, Gibé, Ethiopia, October 2014 (R. J. Dowsett)
Figure 7. Male African Citril *Crithagra citrinelloides*, Debre Libanos, Ethiopia, October 2014 (R. J. Dowsett)
Figure 8. Male Southern Citril *Crithagra hyposticta*, East Usambara Mountains, Tanzania, October 2009 (© Nik Borrow)

either this firefinch or African Firefinch *L. rubricata*, both of which are known from several localities, and *V. purpurascens* would be an addition to the Ethiopian avifauna. The nearest records are those in Kenya, at Kacheriba (Kacheliba), on the Kongelai escarpment (Payne 1973).

BARKA INDIGOBIRD *Vidua larvaticola*
Ash & Atkins detailed four records at three localities, but added that one of these may relate to Sudan, while the two from Gambela might have involved Fonio Indigobirds *V. camerunensis*. The one certain record (from Machigay, *c.*24 km south of Lake Tana) was attributed to *V. camerunensis* by Payne (1973: 333), where apparently listed also (as Madjingais) from Chad. This is perhaps the specimen attributed to Village Indigobird *V. chalybeata* ('*Hypochera ultramarina ultramarina*') by Cheesman & Sclater (1936: 194) from Dangila. This locality (also known as Dangla) is at 11°16'N, 36°50'E, whereas the coordinates for Machigay were given as *c.*11°25'N, 37°14'E by Ash & Atkins (and in error as 11°30'N, 37°40'E by Payne 1982). Cheesman's headquarters were at Dangila (Cheesman 1928), but reading Cheesman & Sclater (1935–36) it is clear that in October 1926 he travelled by mule from Dangila to Gondar, and the coordinates given by Ash & Atkins place Machigay on the road he would have taken (see also Cheesman & Sclater 1935: 300, 608).

To this record can be added our sighting of a male in breeding dress on the Gibé escarpment on 11 October. Its song included clear copies of the call notes of its known host, Black-faced Firefinch *Lagonosticta larvata*, which was present nearby. Also at Gibé, N. Redman (*in litt.* 2014) had a male in breeding dress respond to playback of the song of *L. larvata*, on 2 December 2011, while M. Mills (*in litt.* 2015) sound-recorded a non-breeding bird in song there in April 2014, which also mimicked Black-faced Firefinch.

WILSON'S INDIGOBIRD *Vidua wilsoni*
On 10 October near the old Gibé bridge a male in breeding dress was seen (Fig. 6), and its vocalisations included good imitations of the song of its known host Bar-breasted Firefinch

Lagonosticta rufopicta (the one certain way of identifying this indigobird in the field). Bar-breasted Firefinch is frequently seen at this locality (M. Mills *in litt.* 2015). The only previous Ethiopian records involve specimens from Gambela (Ash & Atkins).

SOUTHERN CITRIL *Crithagra hyposticta*
Ash & Atkins accepted this species as occurring in seven squares, widely spread over the western half of the country. They thought that it might be a 'rare occasional vagrant', occurring in the same places as its sibling, the common African Citril *C. citrinelloides*. Notwithstanding the details presented by these authors (and through them S. L. Olson of the Smithsonian Institution), we believe the occurrence of a second, sympatric species of citril requires careful investigation. It has long been recognised that immature males of *C. citrinelloides* bear a very close resemblance to *C. hyposticta* (Ogilvie-Grant 1913: 579, when examining Ethiopian specimens). Figs. 7–8 show males of the two species. The known range of *C. hyposticta* reaches north to western Kenya and south-east South Sudan (race *brittoni*), while Dickinson & Christidis (2014) tentatively accept nominate *hyposticta* in western Ethiopia.

We found *C. citrinelloides* on many occasions, from Sululta Plain and Debre Libanos (0938B, D) south to Awassa (0738A) and Bale Mountains National Park (0639D), always including black-faced males, and never once did we hear the distinctive whistled calls of *C. hyposticta*, which we know well from Malaŵi and Zambia, and of which a good recording has been published by Stjernstedt (1996). The vocal descriptions given by Fry & Keith (2004) are confusing; only *frontalis* and *hyposticta* appear to give the call of 3–4 whistles (*cf.* Dowsett & Dowsett-Lemaire 1993)—we did not hear it in Ethiopia, and we know of no-one who has.

SALVADORI'S SEEDEATER *Crithagra xantholaema*
Several were seen on 30 October, some 36 km south-east of Negele (FD-L *et al.*). Ash & Atkins knew of no October record, but the species is probably resident.

NORTHERN STRIPE-BREASTED SEEDEATER *Crithagra striatipectus*
We found a male in full song in a large acacia at Kanta Lodge, Konso, on 14 October (1,430 m). This is a new atlas square and there was no previous record for October (although the species must surely be resident), according to Ash & Atkins, who listed it as *Serinus reichardi striatipectus*. It is a good split from *C. reichardi* (Dickinson & Christidis 2014), and the voice (a rich, trilling song) and ecology differ greatly from that of the miombo endemic *C. reichardi* of south-central Africa. The bird we observed closely presented no feature that might suggest the extralimital Streaky-headed Seedeater *C. gularis*, as suggested by Ash & Atkins, referring to what is now known as Northern (or Senegal) Streaky-headed Seedeater *C. canicapilla*, the nearest population of which is in western Kenya (Turner 2013).

Literature records overlooked by Ash & Atkins (2009)

The following published records did not appear on the maps in Ash & Atkins.

WHITE-CHEEKED TURACO *Tauraco leucotis*. 0637C: a specimen from Kullo on the Omo (Érard & Prévost 1991: 23).

NORTHERN WHITE-FACED OWL *Ptilopsis leucotis*. 0738B: Gambo, a type locality of the race *nigrovertex* (Erlanger 1904: 233).

PINK-BREASTED LARK *Calendulauda poecilosterna*. 0536B: collected on the Sagan River, north of Lake Stephanie (Ogilvie-Grant 1913).

TREE PIPIT *Anthus trivialis*. 0637D: a specimen from Baroda, Lake Abaya (Ogilvie-Grant 1913).

SPOTTED PALM THRUSH *Cichladusa guttata* and **WHITE-BROWED SCRUB ROBIN** *Cercotrichas leucophrys*. 0436B: records from Lake Stephanie (Ogilvie-Grant 1913).

RED-FACED CROMBEC *Sylvietta whytii*. 0436B and 0637D: based respectively on specimens from Lake Stephanie and Baroda, Lake Abaya (Ogilvie-Grant 1913).

NORTHERN CROMBEC *Sylvietta brachyura*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

SINGING CISTICOLA *Cisticola cantans*. 0637C: a specimen from Kullo, Omo River (Lynes 1930: 357).

BORAN CISTICOLA *Cisticola bodessa*. 0536D: Bako (Baka) on the Uma River, Konta (Lynes 1930: 272).

TAWNY-FLANKED PRINIA *Prinia subflava*. 0637B: Loco, Lake Abaya (Friedmann 1937).

PALE PRINIA *Prinia somalica*, **YELLOW-BREASTED APALIS** *Apalis flavida* and **GREY FLYCATCHER** *Bradornis microrhynchus*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

SPOTTED FLYCATCHER *Muscicapa striata*. 0637D: Walamo (Ogilvie-Grant 1913); we found it in the same square on the Uajo River, on 12 October.

EASTERN VIOLET-BACKED SUNBIRD *Anthreptes orientalis*. 0637A: Gudji Mountains, Lake Abaya and Schambala River, Male Land (Neumann 1906).

SCARLET-CHESTED SUNBIRD *Chalcomitra senegalensis*. 0738D: Lake Zwai (Ogilvie-Grant 1913). It is indeed common in that square (e.g., Lake Langano, FD-L *et al.*).

SHINING SUNBIRD *Cinnyris habessinicus*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

BEAUTIFUL SUNBIRD *Cinnyris pulchellus*. 0436B: both Donaldson Smith and Zaphiro collected it at Lake Stephanie (Sharpe 1901, Ogilvie-Grant 1913).

EASTERN BLACK-HEADED ORIOLE *Oriolus larvatus*, **BRUBRU** *Nilaus afer* and **SHELLEY'S STARLING** *Lamprotornis shelleyi*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

BAGLAFECHT WEAVER *Ploceus baglafecht*. 0637C: a specimen from Kullo, Omo River (Ogilvie-Grant 1913).

VITELLINE MASKED WEAVER *Ploceus vitellinus* and **RED-CHEEKED CORDON-BLEU** *Uraeginthus bengalus*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

PURPLE GRENADIER *Granatina ianthinogaster*. Several squares are missing from the map in Ash & Atkins: 0436B and 0436C (respectively Lake Stephanie and northern Lake Rudolf: Ogilvie-Grant 1913); 0637D (Lake Abaya: Friedman 1937). We also found it in square 0436C, at Turmi.

BROWN-RUMPED CANARY *Crithagra tristriata* and **STREAKY SEEDEATER** *C. striolata*. 0637C: specimens from Kullo, Omo River (Ogilvie-Grant 1913).

SOMALI GOLDEN-BREASTED BUNTING *Fringillaria poliopleura*. 0436B: Lake Stephanie (Ogilvie-Grant 1913).

Altitudinal limits that amend those given by Ash & Atkins

Below, we list altitudinal limits that differ by more than 150 m (usually upslope) from those in Ash & Atkins (which are given in brackets); they are based on our observations, except where stated.

Somali Courser *Cursorius somalensis* (–1,000 m) 1,450 m (Soda Plain); Ring-necked Dove *Streptopelia capicola* (–1,530 m) 1,920 m (near Kulito); Blue-spotted Wood Dove *Turtur afer* (–1,820 m) 2,450 m (Debre Libanos); Donaldson Smith's Nightjar *Caprimulgus donaldsoni* (–1,370 m) 1,520 m (Negele) and 1,680 m (Yabello); Cinnamon-chested (Blue-breasted) Bee-eater *Merops lafresnayii* (–1,830 m) 2,380 m (Debre Libanos monastery); Yellow-fronted Tinkerbird *Pogoniulus chrysoconus* (–1,820 m) 2,450 m (Harenna forest and Menagesha); Nubian Woodpecker *Campethera nubica* (–2,120 m) 2,350 m (Debre Libanos monastery); Red-faced Cisticola *Cisticola erythrops* (–2,120 m) 2,400 m (Debre Libanos); Tawny-flanked Prinia *Prinia subflava* (above 750 m) 400 m (Lake Dipa); Grey-backed Camaroptera *Camaroptera brachyura* (–2,120 m) 2,380 m (Debre Libanos monastery); Brown Babbler *Turdoides plebejus* (above 700 m) 400 m (Lake Dipa); Spotted Creeper *Salpornis salvadori* (above 1,820 m) 1,660 m (Awassa); Grey-backed Fiscal *Lanius excubitoroides* (–2,000 m) 2,460 m (near Dodola); White Helmet-shrike *Prionops plumatus* (above 900 m) 400 m (Lake Dipa); Black-crowned Tchagra *Tchagra senegalus* (–2,000 m) 2,350 m (Jemma escarpment); Slate-coloured Boubou *Laniarius funebris* (above 910 m) 400 m (Lake Dipa); Black-headed Gonolek *L. erythrogaster* (above 700 m) 400 m (Lake Dipa; also collected on the lower Omo by Donaldson Smith, 22 December 1899: Sharpe 1901, see Donaldson Smith 1900 for his itinerary); Fork-tailed Drongo *Dicrurus adsimilis* (–1,820 m) 2,030 m (Weliso); Somali Crow *Corvus edithae* (–2,500 m) 3,120 m (Dinsho); Slender-billed Starling *Onychognathus tenuirostris* (1,820–3,700 m) 1,660 m (Awassa), 3,940 m (Sanetti Plateau); Snowy-crowned Robin Chat *Cossypha niveicapilla* (above 750 m) 400 m (Lake Dipa); Spotted Palm Thrush *Cichladusa guttata* (–1,500 m) 1,680 m (Yabello); Lead-coloured Flycatcher *Myioparus plumbeus* (above 750 m) 400 m (Lake Dipa); Spectacled Weaver *Ploceus ocularis* (–1,890 m) *c.*2,300 m (Harenna Forest); Black-winged Bishop *Euplectes hordeaceus* (–1,240 m) 1,520 m (Lomi stream); Cinnamon-breasted Rock Bunting *Fringillaria tahapisi* (–1,990 m) 2,400 m (Jemma escarpment).

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Appendix 1

Additions to the species atlas maps in Ash & Atkins (2009), based on records in 2014. An asterisk (*) denotes confirmation of a square record plotted as uncertain by Ash & Atkins.

Black-necked Grebe *Podiceps nigricollis* 0536A, 0537D; Squacco Heron *Ardeola ralloides* 0538C, 0539B; Cattle Egret *Bubulcus ibis* 0539B; Intermediate Egret *Ardea intermedia* 0539B; Black-headed Heron *A. melanocephala* 0739A; Hamerkop *Scopus umbretta* 0536A; Yellow-billed Stork *Mycteria ibis* 0439C; Eurasian Spoonbill *Platalea leucorodia* 0536A; African Black Duck *Anas sparsa* 0938D; Northern Shoveler *Spatula clypeata* 0539B; African Fish Eagle *Haliaeetus vocifer* 0637D; Black-breasted Snake Eagle *Circaetus pectoralis* 0539B, 0639B; Brown Snake Eagle *C. cinereus* 0438C; Western Marsh Harrier *Circus aeruginosus* 0539B, 0639C; Pallid Harrier *C. macrourus* 0537A; Montagu's Harrier *C. pygargus* 0639D*; Gabar Goshawk *Micronisus gabar* 0538C; Ovambo Sparrowhawk *Accipiter ovampensis* 0436D, 0536A*; African Goshawk *A. tachiro* 0536A; Common Buzzard *Buteo buteo* 0438A, 0536A; Verreaux's Eagle *Aquila verreauxii* 0739A; Martial Eagle *Polemaetus bellicosus* 0436C; African Pygmy Falcon *Polihierax semitorquatus* 0537C; Grey Kestrel *Falco ardosiaceus* 0438C, 0539B; Eurasian Hobby *F. subbuteo* 0438A; Sooty Falcon *F. concolor* 0537D; Lanner Falcon *F. biarmicus* 0539D; Common Quail *Coturnix coturnix* 0738B; Red-knobbed Coot *Fulica cristata* 0539B; Common Crane *Grus grus* 0738D; Collared Pratincole *Glareola pratincola* 0539B; Three-banded Plover *Charadrius tricollaris* 0739A; Spur-winged Lapwing *Vanellus spinosus* 0539B; Green Sandpiper *Tringa ochropus* 0539B; White-winged Black Tern *Chlidonias leucopterus* 0539B; Black-faced Sandgrouse *Pterocles decoratus* 0438B; Speckled Pigeon *Columba guinea* 0436C, 0536A; White-collared Pigeon *C. albitorques* 0838B; Lemon Dove *Aplopelia larvata* 0738D; Dusky Turtle Dove *Streptopelia lugens* 0837B; Emerald-spotted Wood Dove *Turtur chalcospilos* 0637D; Bruce's Green Pigeon *Treron waalia* 0539B; Orange-bellied Parrot *Poicephalus rufiventris* 0637D; Levaillant's Cuckoo *Clamator levaillantii* 0539B; Common Cuckoo *Cuculus canorus* 0536A*; Klaas's Cuckoo *Chrysococcyx klaas* 0539B; White-browed Coucal *Centropus superciliosus* 0637D; Barn Owl *Tyto alba* 0938D; African Scops Owl *Otus senegalensis* 0436D; Northern White-faced Owl *Ptilopsis leucotis* 0436D; Cape Eagle Owl *Bubo capensis* 0739A; Long-eared Owl *Asio otus* (*abyssinicus*) 0838D; Donaldson Smith's Nightjar *Caprimulgus donaldsoni* 0539B; Plain Nightjar *C. inornatus* 0438C; Common Swift *Apus apus* 0438A; Woodland Kingfisher *Halcyon senegalensis* 0537C; Blue-cheeked Bee-eater *Merops persicus* 0837B; European Bee-eater *M. apiaster* 0436D, 0438A, 0537A, 0737B, 0738C; European Roller *Coracias garrulus* 0738A; Lilac-breasted Roller *C. caudatus* 0436C; Violet Wood-hoopoe *Phoeniculus damarensis* 0436C, 0536A; Black Scimitarbill *Rhinopomastus aterrimus* 0436D, 0536B; Hoopoe *Upupa epops* 0438A; Hemprich's Hornbill *Tockus hemprichii* 0837B; Yellow-fronted Tinkerbird *Pogoniulus chrysoconus* 0938D; Red-fronted Barbet *Tricholaema diademata* 0536A; Black-billed Barbet *Lybius guifsobalito* 0436D; Red-and-yellow Barbet *Trachyphonus erythrocephalus* 0539B; D'Arnaud's Barbet *T. darnaudii* 0539B; Greater Honeyguide *Indicator indicator* 0539B, 0637D; Lesser Honeyguide *I. minor* 0536A, 0637D; Singing Bush Lark *Mirafra cantillans* 0536A; Fawn-coloured (Foxy) Lark *Calendulauda africanoides* (*alopex*) 0539B; Common Sand Martin *Riparia riparia* 0539B, 0837B; African Rock Martin *Ptyonoprogne fuligula* 0539D; Wire-tailed Swallow *Hirundo smithii* 0537A; Common House Martin *Delichon urbicum* 0539B; Yellow Wagtail *Motacilla flava* 0536B; Grassland Pipit *Anthus cinnamomeus* 0539B; Tree Pipit *A. trivialis* 0439C; Abyssinian Longclaw *Macronyx flavicollis* 0738B; White-breasted Cuckoo-shrike *Ceblepyris pectoralis* 0436D; Northern Brownbul *Phyllastrephus strepitans* 0539B; African Thrush *Turdus pelios* 0436D; Bare-eyed Thrush *T. tephronotus* 0539B; Sprosser *Luscinia luscinia* 0837B; Snowy-crowned Robin Chat *Cossypha niveicapilla* 0536A; White-browed Robin Chat *C. heuglini* 0738D; Spotted Palm Thrush *Cichladusa guttata* 0439C, 0637D; White-browed Scrub Robin *Cercotrichas leucophrys* 0438B, 0637D; Pied Wheatear *Oenanthe pleschanka* 0438B; Black-eared Wheatear *O. hispanica* 0438A; Isabelline Wheatear *O. isabellina* 0537D; Little Rush Warbler *Bradypterus baboecala* 0940A; Marsh Warbler *Acrocephalus palustris* 0837B; Great Reed Warbler *A. arundinaceus* 0738A; Icterine Warbler *Hippolais icterina* 0738D*; Red-faced Crombec *Sylvietta whytii* 0436D; Banded Parisoma *Sylvia boehmi* 0438B; Rattling Cisticola *Cisticola chiniana* 0438B, 0637D; Boran Cisticola *C. bodessa* 0536B; Red-faced Cisticola *C. erythrops* 0537A; Singing Cisticola *C. cantans* 0639D, 0837D, 0838A; Tawny-flanked Prinia *Prinia subflava* 0537C, 0637D, 0838A; Red-fronted Warbler *P. rufifrons* 0536A*; Grey-backed Camaroptera *Camaroptera brachyura* 0436D; Northern Black Flycatcher *Melaenornis edolioides* 0438A; Spotted Flycatcher *Muscicapa striata* 0536A, 0637D; Lead-coloured Flycatcher *Myioparus plumbeus* 0637D; Pygmy Batis *Batis perkeo* 0439C; Common Wattle-eye *Platysteira cyanea* 0837D; Northern Grey Tit *Melaniparus thruppi* 0438B, 0536A; Eastern Violet-backed Sunbird *Anthreptes orientalis* 0637D; Collared Sunbird *Hedydipna collaris* 0637D; Scarlet-chested Sunbird *Chalcomitra senegalensis* 0738D; Variable Sunbird *Cinnyris venustus* 0539B, 0838A; Marico Sunbird *C. mariquensis* 0637D; Copper Sunbird *C. cupreus* 0938D*; Tacazze Sunbird *Nectarinia tacazze* 0639C; Abyssinian White-eye *Zosterops abyssinicus* 0539B, 0637B; Yellow White-eye *Z. senegalensis* 0536A; Eastern Black-headed Oriole *Oriolus larvatus* 0438A, 0840C; Red-backed Shrike *Lanius collurio* 0637D; Isabelline Shrike *L. isabellinus* 0439C; Great Grey Shrike *L. excubitor* 0539B, 0637D; Grey-backed Fiscal *L. excubitoroides* 0639C; Brubru *Nilaus afer* 0837B; Three-streaked Tchagra *Tchagra jamesi* 0840C; Slate-coloured Boubou *Laniarius funebris* 0438B, 0637D; Sulphur-breasted Bushshrike *Chlorophoneus sulfureopectus* 0637D, 0837B; Grey-headed Bushshrike *Malaconotus blanchoti* 0438B, 0637D, 0837B; Stresemann's Bush-crow *Zavattariornis stresemanni* 0438A, 0538A; Pied Crow *Corvus albus* 0436C; Bristle-crowned Starling *Onychognathus salvadorii* 0539B; Lesser Blue-eared Starling *Lamprotornis chloropterus* 0436C; Yellow-spotted Petronia *Gymnoris pyrgita* 0436D; Baglafecht Weaver *Ploceus baglafecht* 0838A; Black-

necked Weaver *P. nigricollis* 0536B; Lesser Masked Weaver *P. intermedius* 0439C; Rüppell's Weaver *P. galbula* 0838A; Red-headed Weaver *Anaplectes rubriceps* 0438B, 0637D; Red-billed Quelea *Quelea quelea* 0439C, 0539B; Green-winged Pytilia *Pytilia melba* 0436C, 0738D; Jameson's Firefinch *Lagonosticta rhodopareia* 0637D; Red-cheeked Cordon-bleu *Uraeginthus bengalus* 0436C; Purple Grenadier *Granatina ianthinogaster* 0436C, 0637D; Grey-headed Silverbill *Euodice griseicapilla* 0536B; Cut-throat Finch *Amadina fasciata* 0439C; Village Indigobird *Vidua chalybeata* 0539D; Purple Indigobird *V. purpurascens* 0637D; Barka Indigobird *V. larvaticola* 0837B; Wilson's Indigobird *V. wilsoni* 0837B; Eastern Paradise Widow *V. paradisaea* 0439C; Brown-rumped Seedeater *Crithagra tristriata* 0639C; Northern Stripe-breasted Seedeater *C. striatipectus* 0537A.

Appendix 2

Gazetteer of localities mentioned in the text, with the 30-minute square to which we allocate it in Ethiopia (and in brackets the square numbers used by Ash & Atkins). Coordinates and altitudes (the latter given to the nearest 10 m) have, where possible, been confirmed personally by a GPS reading.

Locality	Coordinates	Square	Altitude (m)
Agere Maryam	05°38′N, 38°14′E	0538C (109a)	1,860
Archer's Post, *Kenya*	00°39′N, 37°41′E		
Arero, Sidamo	04°42′N, 38°45′E	0438D (120b)	1,360
Aveve, Kollu Province		0938A (58c)	
Awash Gorge, Awash National Park	@ 08°51′N, 40°01′E	0840C (71a)	910
Baroda, near Lake Abaya	06°32′N, 37°46′E	0637D (96b)	1,400
Bilen Lodge, Awash National Park	09°28′N, 40°19′E	0940A (60c)	730
Bishangari, Lake Langano	07°32′N, 38°48′E	0738D (83b)	1,600
Dangila	11°16′N, 36°50′E	1136B (38d)	2,100
Dawa River	04°52′N, 39°19′E	0439C (121a)	740
Debre Libanos (Ethio-German Park Hotel)	09°44′N, 38°49′E	0938D (58b)	2,490
Debre Libanos Monastery	09°43′N, 38°51′E	0938D (58b)	2,380
Dinsho (Gurie)	07°06′N, 39°47′E	0739B (84d)	3,100
Dodola	06°59′N, 39°11′E	0639C (98a)	2,460
Gambela	08°08′N, 34°34′E	0834B (65d)	450
Gambo	07°26′N, 38°52′E	0738B (83d)	2,290
Gamo, near Lake Abaya	*c.*06°20′N, 37°30′E	0637B (96d)	
Genale River	05°30′N, 39°43′E	0539B (110d)	880
Gibé River, Jimma		0837A (68c)	
Gibé bridge (old)	08°14′N, 37°35′E	0837B (68d)	1,170
Gibé escarpment	@ 08°16′N, 37°37′E	0837B (68d)	1,430
Goba	07°01′N, 39°59′E	0739B (84d)	2,650
Gondar (Gonder)	12°36′N, 37°30′E	1237C (29a)	2,260
Gore	08°09′N, 35°32′E	0835B (66d)	
Gudji Mountains, Lake Abaya	06°14′N, 37°23′E	0637A (96c)	2,300–3,300
Harenna forest, Bale Mountains	@ 06°45′N, 39°43′E	0639D (98b)	2,540
Jemma escarpment	@ 09°50′N, 38°53′E	0938D (58b)	2,360
Jemma Valley	@ 09°55′N, 38°55′E	0938D (58b)	1,350
Kacheriba, Kongelai 'scarp, *Kenya*	01°29′N, 35°01′E		
Kanta Lodge, Konso	05°20′N, 37°27′E	0537A (108c)	1,430
Kaske River near Turmi	04°58′N, 36°31′E	0436D (118b)	860
Kolosia (or Kolothia), Turkana, *Kenya*	01°38′N, 35°46′E		
Kulito	07°19′N, 38°05′E	0738A (83c)	1,780
Kullo on the lower Omo	06°39′N, 37°10′E	0637C (96a)	660
Lake Abiata (Abiata-Shalla National Park)	07°39′N, 38°38′E	0738D (83b)	1,530
Lake Awassa	07°03′N, 38°26′E	0738A (83c)	1,660
Lake Chamo	05°56′N, 37°32′E	0537D (108b)	1,090
Lake Dipa	05°10′N, 36°12′E	0536A (107c)	400
Lake Langano	@ 07°32′N, 38°48′E	0738D (83b)	1,600
Lake Zwai	07°56′N, 38°43′E	0738D (83b)	1,640
Liben Plain	@ 05°16′N, 39°41′E	0539B (110d)	1,580
'Little' Kaske River near Turmi	04°58′N, 36°29′E	0436C (118a)	930
Loco, Lake Abaya	06°20′N, 37°55′E	0637B (96d)	1,180
Lomi stream	09°57′N, 38°54′E	0938D (58b)	1,510
Machigay	*c.*11°25′N, 37°14′E	1137A (39c)	2,050
Mago National Park		0536A,C (107c,a)	
Mega	04°03′N, 38°19′E	0438A (120c)	1,650
Melka Ghebdu	09°34′N, 39°50′E	0939D (59b)	
Menagesha forest	08°58′N, 38°32′E	0838D (69b)	2,450–2,850
Metu	08°18′N, 35°35′E	0835B (66d)	

Murle Lodge, Omo River	05°10'N, 36°12'E	0536A (107c)	430
Nechisar Plain, Nechisar National Park	@ 05°53'N, 37°39'E	0537D (108b)	1,230
Negele	05°20'N, 39°35'E	0539B (110d)	1,520
Sagan River, north of Lake Stephanie	c.05°10'N, 36°50'E	0536B (107d)	
Sanetti Plateau area	c.06°55'N, 39°55'E	0639D (98b)	3,100–4,000
Schambala River, Male Land	c.06°30'N, 37°12'E	0637A (96c)	
Simbo Lodge, Lake Langano	07°33'N, 38°41'E	0738D (83b)	1,570
Soda Plain south-east of Yabello	c.04°10'N, 38°17'E	0438A (120c)	1,520
Sodo	06°52'N, 37°46'E	0637D (96b)	2,000
Sululta Plain	c.09°20'N, 38°45'E	0938B (58d)	2,570
Tepi	07°12'N, 35°25'E	0735A (80c)	
Turmi Lodge and town	04°58'N, 36°29'E	0436C (118a)	930
Uajo River, south of Sodo	06°34'N, 37°49'E	0637D (96b)	1,260
Uma River, Konta	c.05°47'N, 36°34'E	0536D (107b)	
Walamo	06°50'N, 37°40'E	0637D (96b)	1,900
Wadera	05°45'N, 39°19'E	0539C (110a)	1,760
Weliso (Wolisso)	08°32'N, 37°59'E	0837D (68b)	2,030
Weyto	05°22'N, 36°59'E	0536B (107d)	580
Wondo Genet	07°04'N, 38°39'E	0738B (83d)	1,760
Yabello (Borana Lodge)	04°51'N, 38°10'E	0438C (120a)	1,680
Zoula River, Uba	c.06°09'N, 36°53'E	0636B (95d)	

Molecular analysis of a storm petrel specimen from the Marquesas Islands, with comments on specimens of *Fregetta lineata* and *F. guttata*

by Alice Cibois, Jean-Claude Thibault, Mary LeCroy & Vincent Bretagnolle

Summary.—An old museum specimen of a storm petrel from the Marquesas Islands (French Polynesia) was sampled genetically. This specimen has been alternatively attributed to Black-bellied Storm Petrel *Fregetta tropica*, or described as a new taxon. Its plumage also recalls the recently rediscovered New Zealand Storm Petrel *F. maoriana*. However, molecular phylogenetic analysis revealed that this specimen is closely related to some individuals of White-bellied Storm Petrel *F. grallaria*, which species is apparently non-monophyletic.

Storm petrels are small seabirds divided into two families, the Oceanitidae (Austral storm petrels) and Hydrobatidae (Northern storm petrels), which are apparently not sister taxa (Hackett *et al.* 2008). Austral storm-petrels have short, round wings, usually square-ended tails and long legs. They typically forage while gliding slowly with their legs dangling on the surface of the ocean. Systematics within the family are complex with five genera and eight species recognised (Dickinson & Remsen 2013), including recently rediscovered species (e.g. New Zealand Storm Petrel *Fregetta maoriana*; Stephenson *et al.* 2008), new species (e.g. Pincoya Storm Petrel *Oceanites pincoyae*; Harrison *et al.* 2013) and potentially undescribed forms (Shirihai *et al.* 2015), while previously established taxonomy is strongly debated (e.g. species delimitation of Black-bellied Storm Petrel *Fregetta tropica* and White-bellied Storm Petrel *F. grallaria*, which might breed sympatrically on Gough Island, South Atlantic: Brooke 2004, Flood & Fisher 2011, Howell 2012).

New Zealand Storm Petrel belongs to the 'streaked' white-bellied forms of storm petrels, the so-called '*pealea*' phenomenon described *c.*60 years ago (genera *Fregetta*, *Nesofregetta* and *Garrodia*: Murphy & Snyder 1952). Five particular '*pealea*' specimens held in various museums have confused the systematics of South Pacific storm petrels for decades (*cf.* Stephenson *et al.* 2008 for a complete review), being assigned to three different genera over the years, *Fregetta, Thalassidroma* or *Pealea* (taxon *lineata*). The situation has been much clarified with the rediscovery of *Fregetta maoriana*, to which three of the five specimens refer, including the type of *F. maoriana* (Robertson *et al.* 2011). The other two specimens, according to Murphy & Snyder (1952), are a streaked bird presumed to be *F. grallaria*, collected off the Marquesas (see below) and another streaked specimen, which is considered to be a *F. tropica*, collected at Upolu, Samoa, in 1839 by Peale (see Discussion).

Taxonomic placement of *F. maoriana* was ambiguous based on plumage comparison, so a genetic analysis was conducted to assign this taxon to genus (Robertson *et al.* 2011). Here, we address the identity of the Marquesan specimen using a similar approach. This bird was collected at sea off Ua Pou (Marquesas Islands) on 15 September 1922 by R. H. Beck during the Whitney South Sea Expedition (WSSE). A female, it was registered in the American Museum of Natural History, New York (AMNH 194110) under the species name *Fregetta lineata* (Peale, 1848), now a junior synonym of *Fregetta tropica* (Gould, 1844). According to Murphy (1924), who cited the WSSE logbook: 'the bird was feeding in a streak of oily water in company with large numbers of *Bulweria* [petrels] and *Fregetta grallaria*'.

Figure 1. Specimen AMNH 194110, (a) ventral view and (b) side view of head (Matthew Shanley / © AMNH), and (c) ventral view of specimen USNM 15713 (Vincent Bretagnolle)

Mathews (1933) re-examined the specimen and assigned the bird to the new taxon, *Fregetta guttata* (not *Fregettornis guttata*; Murphy & Snyder 1952), based on the presence of dark belly streaking (Fig. 1a, b), which was thought to be absent in White-bellied Storm Petrel at that time. Murphy & Snyder (1952), however, found this plumage difference insufficient for recognition of a new taxon and assigned this specimen instead to *F. grallaria*. Overall, Murphy & Snyder (1952) and Jouanin & Mougin (1979) considered all of the '*lineata*' specimens to be aberrant plumages of distinct species of storm petrels. However, we found the assignment of AMNH 194110 to *F. grallaria* to be questionable, first because this species has not otherwise been recorded in the Marquesas (thus questioning Beck's identification in the field), apart from subfossil bones attributed to *Fregetta* sp. (Steadman 2006), and second because the specimen's odd plumage recalls the streaked belly of *F. maoriana*. Clearly, the identity of this specimen, based on its provenance and plumage, is uncertain. Here we address this issue using phylogenetic analysis of mitochondrial (cytochrome-*b*) DNA of this specimen and other storm petrels in the Oceanitidae and Hydrobatidae.

Material and Methods

A small fragment of toe pad was sampled from AMNH 194110. It was washed with sterile water before extraction, and total genomic DNA was extracted from small pieces

TABLE 1
Primers used in this study.

| Primer name	5'-3' sequence	Reference
8L (L14990)	CATCCAACATCTCTGCTTGATGAAA	Modified from Kocher et al. (1989)
33H	TCGGCCGATGTGGAGGTAGATGC	Cibois et al. (2007)
L154a	CAAACGGAGCCTCATTCTT	Robertson et al. (2011)
B37H	CATTCTACGATGGTTTGGCC	This study
B35L	AAAGAAACCTGAAACACAGG	This study
36H	TGGGTTGTCTACTGAGAA	Cibois et al. (2007)
37L	GGCCAAACCTTAGTAGAATG	Cibois et al. (2007)
38H	GGAGTAGTATGGGTGGAATGGGA	Cibois et al. (2007)
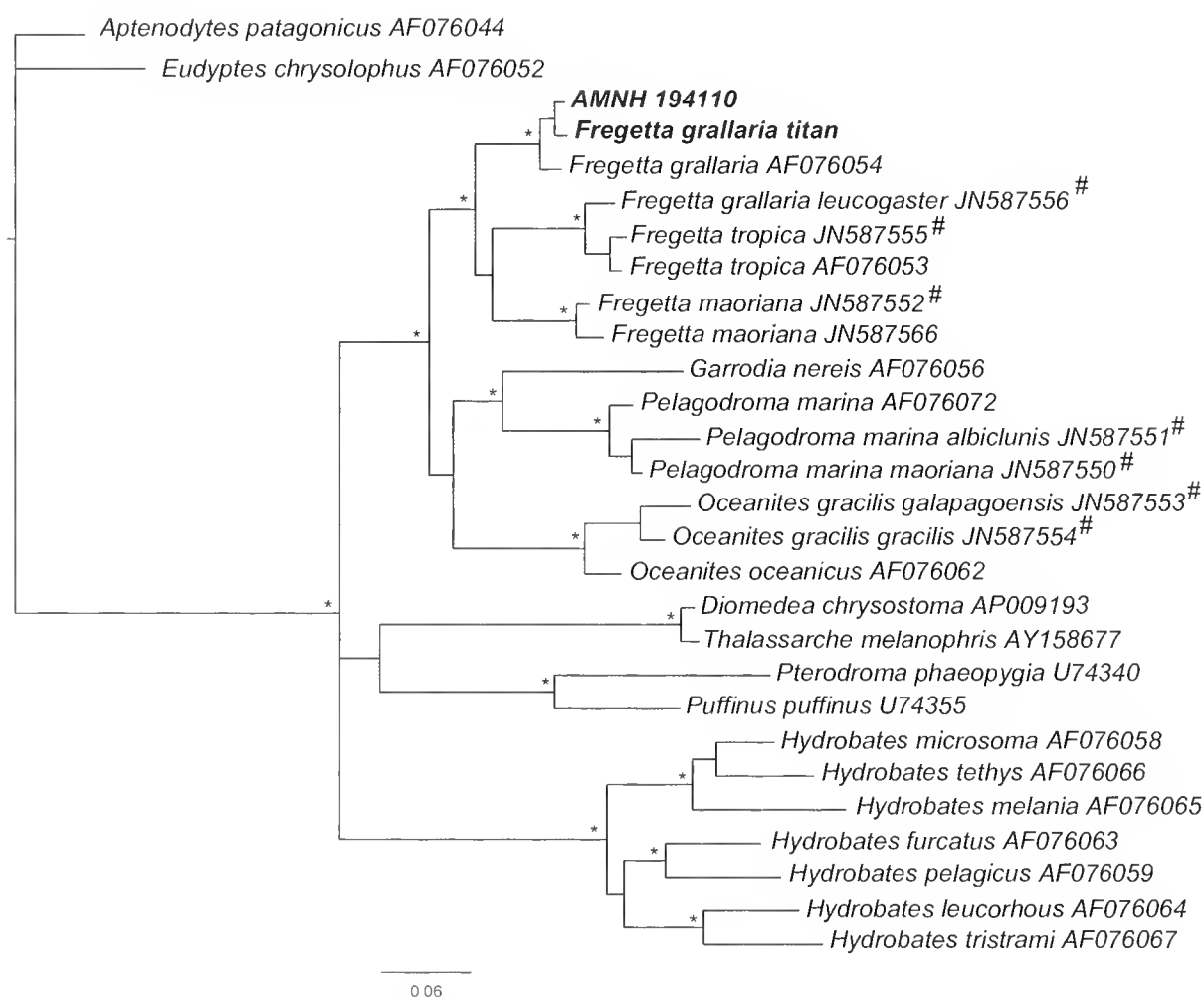
Figure 2. Phylogenetic tree estimated using Bayesian inference and cytochrome-*b* sequences. Posterior probabilities superior to 0.95 are indicated by an asterisk. GenBank numbers are indicated beside the taxon name and new sequences are in bold. # indicates short sequences (132 bp) from Robertson et al. (2011).

(0.5–1.0 mm²) of skin using a commercial kit (DNeasy Tissue Kit; Qiagen, Valencia, CA). Standard extraction protocols were followed except that the time of proteinase digestion was increased from two to 12 hours, with an additional volume (20 µl) of proteinase K. All tubes and reagents were UV-treated for 30 minutes before use and extraction tubes containing no sample were used as a control for contamination. DNA extracted from museum specimens was degraded, so fragment sizes for amplification were small (c.200 bp). Using standard

TABLE 2

Pair-wise sequence divergence found in cytochrome-*b* sequences (% uncorrected values). The individuals studied here are indicated in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. *Fregetta grallaria titan* [*]	-													
2. *Fregetta grallaria* AF076054 [*][a]	2.0													
3. *Fregetta maoriana* JN587552 [b]	6.1	6.1												
4. *Fregetta maoriana* JN587566 [*][b]	6.8	7.5	0.8											
5. *Pelagodroma marina maoriana* JN587550 [*][b]	7.6	9.1	7.6	6.8										
6. *Pelagodroma marina albiclunis* JN587551 [*][b]	9.1	7.6	9.1	9.8	3.0									
7. *Pelagodroma marina* AF076072 [*][a]	8.4	8.8	7.6	10.7	1.5	4.5								
8. *Fregetta grallaria leucogaster* JN587556 [b]	9.1	9.1	6.1	6.8	10.6	10.6	10.6							
9. *Fregetta tropica* JN587555 [*][b]	9.8	9.8	5.3	6.1	9.8	11.4	9.8	2.3						
10. *Fregetta tropica* AF076053 [*][a]	8.4	7.4	6.1	8.1	10.6	10.6	10.8	1.5	0.8					
11. *Garrodia nereis* AF076056 [*][a]	9.0	9.9	5.3	11.2	9.1	7.6	9.6	5.3	6.1	10.1				
12. *Oceanites gracilis galapagoensis* JN587553 [b]	9.8	9.8	8.3	9.1	9.8	11.4	9.8	8.3	7.6	8.3	10.6			
13. *Oceanites gracilis gracilis* JN587554 [b]	10.6	10.6	9.1	9.8	10.6	12.1	10.6	9.1	8.3	9.1	11.4	2.3		
14. *Oceanites oceanicus* AF076062 [*][a]	9.5	9.3	9.8	9.6	11.4	12.9	9.4	9.8	9.1	8.9	10.8	4.5	3.8	
15. *Fregetta* sp. AMNH 194110	1.3	2.2	5.3	6.3	6.8	8.3	7.9	8.3	9.1	8.3	9.2	9.1	9.8	9.7

[*] no voucher specimen; [a] Nunn & Stanley (1998); [b] Robertson *et al.* (2011).

protocols, we also sequenced one individual of *Fregetta grallaria titan* from Rapa, Austral Islands (from a feather obtained by B. Fontaine in December 2002 on Tarakoi Islet), in order to obtain a longer sequence than that available on Genbank (JN587557, only 132 bp). Several primers for the cytochrome-*b* gene were designed specifically for this study (Table 1). PCR amplifications were performed in 25 µl reactions with 2 µl of template and 0.4 µM final concentration for primers, using Qiagen Taq (no PCR additives). The thermo-cycling procedure commenced with an initial denaturation of three minutes at 95°C, followed by 40 cycles of 30 seconds at 95°C, 40 seconds at annealing temperature (46–50°C depending on the primer) and 40 seconds at 72°C for elongation. PCR products were purified using a Qiagen QIAquick purification kit and sequenced in both directions at a contract sequencing facility (Macrogen, Seoul, South Korea) on an ABI3730 XL automatic DNA sequencer, using the same primers as used in PCR. Contiguous sequences derived from the set of sequence fragments were created using Sequencher (Genecodes, Ann Arbor, MI). Sequences were aligned to all storm petrel cytochrome-*b* sequences available on GenBank as well as those of four other Procellariiformes (two albatrosses, one *Pterodroma* petrel and one *Puffinus* shearwater) and two Sphenisciformes from the following studies: Nunn *et al.* (1996), Nunn & Stanley (1998), Slack *et al.* (2006), Watanabe *et al.* (2006), Robertson *et al.* (2011). All species of Oceanitidae were represented in the dataset except Polynesian Storm Petrel *Nesofregetta fuliginosa*, for which no cytochrome-*b* sequence was available. The two Sphenisciformes were used as outgroup, following the phylogeny in Hackett *et al.* (2008). The data were subjected to Bayesian inference using MrBayes 3.2.1 (Ronquist & Huelsenbeck 2003), with models selected using MrModeltest 2.3 for each codon position, using the AIC criterion (Nylander 2004). We conducted two independent runs of four Markov chains for one million generations each. Markov chains were sampled every 1,000 generations, with a 10% burn-in period.

Results and Discussion

Partial cytochrome-*b* gene sequences of 557 bp were obtained for *Fregetta grallaria titan* and for AMNH 194110, deposited in GenBank under accession nos. KP857579 and KP857580, respectively. The alignment was straightforward with no indels, as expected for a protein-coding gene. We translated the nucleotide sequences to proteins using Mega (Tamura *et al.* 2013) and found no stop codons. We detected no contamination in the negative controls. Results from the AIC criterion in MrModeltest supported the GTR + I for the first codon position, and the GTR + I + G model for the second and third codon positions (General Time Reversible, Proportion Invariant, and Gamma: Lanave *et al.* 1984, Rodríguez *et al.* 1990). In the phylogenetic tree obtained using MrBayes (Fig. 2), the two families Oceanitidae and Hydrobatidae were found to be monophyletic, but because a single gene was used, the relationships between families within Procellariiformes were poorly supported (i.e. posterior probabilities <0.95) and lie beyond the scope of this paper. Within Oceanitidae, *Garrodia* and *Pelagodroma* were sister taxa, as in Robertson *et al.* (2011), but the remaining relationships between genera were not supported. At species level, AMNH 194110 belonged with strong support to genus *Fregetta*, and more specifically formed a clade with *F. grallaria titan* and *F. grallaria* ssp. from the East Pacific (Genbank sequence AF076054 without voucher specimen; G. Nunn pers. comm.). The lowest sequence divergence between AMNH 194110 and any other individual was with *F. g. titan* (1.3%, vs. 2.2% for *F. grallaria* ssp. AF076054; Table 2), and the two are sister taxa, albeit without strong support (posterior probability of 0.65). However, another individual supposedly of the same species, *F. g. leucogaster* (JN587556 from Gough Island; sequences from a toe pad of NHMUK 1953.55.101; Robertson *et al.* 2011), did not belong to this group and clustered with strong support with *F. tropica*. Finally, we found strong support for the two *Oceanites* as sister species, and for the group formed by the three *Pelagodroma marina* individuals.

Although a single mitochondrial gene is clearly insufficient to elucidate with certitude relationships within Oceanitidae, these results suggested several directions where future molecular research should be directed. First, placement of AMNH 194110, a bird with dark belly streaking, closely related to the white-bellied subspecies *titan* from Rapa, might support Murphy & Snyder's (1952) conclusion that this specimen is closely related to, and might be, *F. grallaria*. According to Murphy & Snyder (1952), wing length of AMNH 194110 (165 mm) is intermediate between those of *titan* and nominate (184 mm and 156 mm for females, respectively). Consequently, although our results assign AMNH 194110 to *F. grallaria*, its attribution at subspecies level is uncertain, pending further sampling of *grallaria* at other localities (e.g., *F. g. segethi*, breeding on the Juan Fernández and Desventuradas Islands, was not included in our analysis). One also cannot eliminate the possibility that this specimen belongs to another taxon, closely related to but distinct from *F. grallaria*. This female, possibly breeding (according to its enlarged gonads, as reported on the specimen's label), was collected in waters off the Marquesas Islands, 2,070 km from the closest known breeding areas on Rapa, suggesting either long-distance dispersal or the possibility of another breeding population somewhere in the Marquesas. The presence of subfossil bones attributed to *Fregetta* on two Marquesan islands (Ua Huka and Tahuata; Steadman 2006), provides support for past presence of this taxon in the archipelago.

Second, *F. grallaria*, as currently defined, may not be a monophyletic taxon. In our cytochrome-*b* phylogeny, the individual of *F. g. leucogaster* from Gough Island (NHMUK 1953.55.101: Robertson *et al.* 2011) is closely related to two *F. tropica*: JN587555 from South Island, New Zealand (no voucher specimen: Robertson *et al.* 2011) and AF076053 from Marion Island, south-west Indian Ocean (no voucher specimen: Nunn & Stanley 1998; G.

Nunn pers. comm.). This group differs by *c*.9% from sequences of other *F. grallaria* (Table 2), a degree of divergence much greater than that typically reported among Procellariform species (Austin *et al.* 2004). This result was previously found by Robertson *et al.* (2011; their Table 1), but they did not include *leucogaster* in their phylogenetic tree and did not mention it in their discussion. As noted above, the taxonomic status of *Fregetta* species breeding on Gough Island is poorly understood, with two species with white bellies (*F. tropica melanoleuca* and *F. grallaria leucogaster*) that might breed in sympatry (Brooke 2004, Flood & Fisher 2011).

Finally, the fifth streaked specimen of the '*pealea*' series (Murphy & Snyder 1952) is now in the Smithsonian Institution, Washington DC, collection (USNM 15713; Fig. 1c); it is the type of *Thalassidroma lineata* Peale, 1848, which was synonymised with *F. tropica* by Murphy & Snyder (1952). Although we did not sample that bird genetically, its wing length is similar to that of AMNH 194110 (166 mm *per* Murphy & Snyder 1952). Thus both are smaller than *titan* but much larger than *F. maoriana* (*c*.148 mm: Stephenson *et al.* 2008). They share with the latter a streaked belly, but we found that AMNH 194110 is distinct genetically from *F. maoriana*. These two '*lineata*' specimens, similar in size and coloration, could therefore represent a distinct taxon within *Fregetta*, but the discovery of additional individuals will be necessary to support this hypothesis.

Our evaluation of the identity of one specimen, based on a single mitochondrial gene, employs an approach similar to barcoding (Frézal & Leblois 2008). Because the cytochrome-*b* phylogeny was consistent with the nuclear tree in Robertson *et al.* (2011), we consider that using this gene to assess the identity of this storm petrel is appropriate. However, we cannot eliminate the possibility of hybridisation between closely related storm petrels, leading to the introgression of mitochondrial genes from one species to another (Rheindt & Edwards 2011), and causing for example the polyphyly of *F. grallaria*. Alternatively, the taxonomic definition of *F. grallaria*, and perhaps *F. tropica*, a species with considerable individual variation in plumage, might not be accurate (Brooke 2004). Further sampling of individuals from multiple locations, as well as a wider array of genes, is clearly required to decipher relationships within these two species.

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Rufous-cheeked Nightjar *Caprimulgus rufigena* behaviour during the breeding season in Zimbabwe

by H. D. Jackson

SUMMARY.—Behaviour of Rufous-cheeked Nightjar *Caprimulgus rufigena*, a summer visitor to southern Africa, was studied in Zimbabwe during two breeding seasons, using radiotracking to follow individuals and locate nests. Males defend territories by regular singing at potential nest sites. Females and other males are attracted to these sites; intruding males are challenged vocally on the ground and during aerial chases; females test possible nest spots, while the resident male watches, sings and/ or follows and displays. No nest is prepared; the eggs, usually two, are laid directly onto the ground. Egg losses are high but replacement clutches are sometimes laid. Females incubate by day, males at night; both may feed or roost outside the territory. Flying insects are caught in short flights from the ground.

Caprimulgidae by virtue of their crepuscular and nocturnal habits, and their cryptic coloration, are difficult to study in the field. While museum specimens of Afrotropical nightjars provide much information concerning their distribution, biometrics, food, relationships, mortality and moult (Jackson 1978, 2000a,b, 2002b,c, 2008), they reveal little about behaviour. Data from captive nightjars can provide clues to natural behaviour (Jackson 2009), but ideally field studies of wild birds are required.

Field studies in Zimbabwe have provided data on five of the seven species occurring there: Fiery-necked Nightjar *Caprimulgus pectoralis* (Jackson 1985, 1987, 2002a,d), Freckled Nightjar *C. tristigma* (Steyn 1971, Jackson 1973a,b, 1985), Square-tailed Nightjar *C. fossii* (Jackson 1985, 1987, 2003), Swamp Nightjar *C. natalensis* (Jackson 1987, Hustler & Carson 1996, Hustler 1997, 2003, Hustler & Mitchell 1997) and Pennant-winged Nightjar *Macrodipteryx vexillarius* (Shaw 1993, Jackson 2003, 2004). As European Nightjar *C. europaeus* does not breed in Zimbabwe, the only local breeder not addressed by these studies is Rufous-cheeked Nightjar *C. rufigena*, a trans-equatorial summer visitor.

Here I describe the breeding-season behaviour of Rufous-cheeked Nightjar, based on radiotracking and Betalights to follow individuals and locate nests. These aids were successfully used in England to study the behaviour of European Nightjar (Cresswell 1985); birds carrying radio packs and Betalights bred normally (B. Cresswell *in litt.* 1986).

Methods

Study area.—Quiet Waters Nature Reserve (20°18′S, 29°59′E) is owned and administered, as part of its conservation scheme, by Falcon College, near Esigodini, Zimbabwe. Descriptions and maps of the geology and topography of the reserve, with checklists of the flora and fauna, by Cunningham (1996) form the basis of this brief summary. Most of the 220-ha reserve (Fig. 1) is underlain by greenstone schists, heavily fractured and impregnated by many quartz veins and a few dolerite dykes. The major feature in the north of the reserve is the Usandisa massif, a prominent steep-sided, boulder-strewn granite kopje with a series of elevated benches and outcrops. South of Usandisa is a gently sloping area of deep, white sandy soils, and to the east of this is a pan, which was almost dry in 1988–89.

TOPOGRAPHY OF QUIET WATERS NATURE RESERVE, FALCON COLLEGE, ESIGODINI, ZIMBABWE
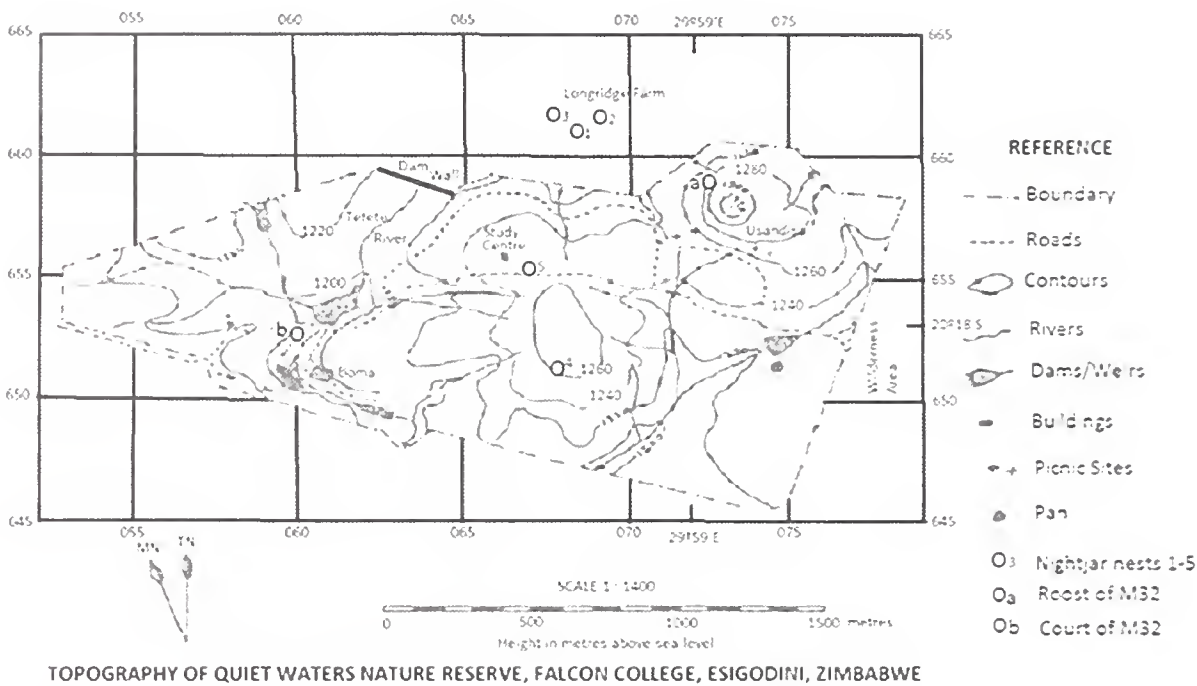
Figure 1. Map of Quiet Waters Nature Reserve, Falcon College, Esigodini, Zimbabwe, adapted from Cunningham (1996), with nightjar data added.

In the centre of the reserve is an oval-shaped hill covered with fragments of white quartz weathered from exposed quartz veins. A study centre, containing natural history specimens and other didactic material, is sited there. The drainage is dominated by the south-flowing Tetete River. Within the reserve the river is dammed in three places and some of its tributaries also have small earth weirs, providing extensive surface water when rains are good.

On schist soils the woody vegetation is fairly uniform, dominated by *Combretum*, *Acacia*, *Diplorhynchus* and *Euclea* spp. Tree species on granite and sandveld are far more diverse and include *Ficus*, *Terminalia*, *Burkea*, *Pterocarpus*, *Parinari* and *Strychnos*. On alluvial soils the riverine vegetation is typified by *Salix* and *Rhus*, while the commonest large tree on the pan is *Acacia sieberana*. Dominant grasses on the sandveld are *Eragrostis* spp., while those on the schist/clay complex are *Themeda*, *Heteropogon* and *Aristida* spp.

Nightjar research.—Some 375 hours, over 49 nights, from mid-September to mid-November 1988 and 1989, were spent in the reserve (Table 1), capturing, ringing, tagging, then tracking and observing nightjars during the breeding season. Observations were made from a vehicle parked 10–15 m from the bird using binoculars, or from a small canvas hide. I glued Betalights (Biotrack, UK), which emit an omnidirectional faint green glow in the dark, to the crowns of some individuals. These devices are tritium-filled capsules, lined with phosphorescent paint; they shine continuously and require no power source. Detailed notes were dictated into a pocket recorder and subsequently transcribed. Night lighting (Jackson 1984) was used to find and trap nightjars. Mist-nets and song playback were also

TABLE 1

Periods during which nightjar research was undertaken in Quiet Waters Nature Reserve.

1988		1989	
September	25–28	September	13–17
October	2–5		19–25
	9–11	October	10–20
	16–18	November	9–17
	23–26		
November	6–9		
	13–15		

used. All birds trapped were ringed for individual identification and weighed to the nearest gram using a Pesola spring balance before release at the capture point.

Radiotracking.—Some Rufous-cheeked Nightjars were also fitted with 2-g radio transmitters (Biotrack, UK) in the 173.2–173.35 MHz frequency band. Transmitter packages were glued to the base of the two central rectrices. I deployed five transmitters in 1988, all on females, specifically to find nests. In 1989 one radio-tagged male was monitored for most of the season. Radiotracking was performed using a Mariner-57 receiver and three-element Yagi antenna. The reserve boundary fence is electrified, so the current had to be turned off before a bird could be tracked across it.

Results

Population density and variety.—In each of the two seasons, the reserve supported *c*.6 pairs of Rufous-cheeked, three pairs of Fiery-necked and two pairs of Freckled Nightjars, based on the dusk song of males in different parts of the reserve. No Square-tailed Nightjar song was heard, despite apparently suitable habitat in the reserve. Insect-like song thought to belong to Pennant-winged Nightjar was actually produced by a small cricket (Gryllidae, *Cophogryllus* sp.). Up to five male Pennant-winged Nightjars were displaying along 1 km of the main road west of the reserve, but none was seen in the reserve. A European Nightjar was observed perched on the boundary fence. Thirteen nightjars were trapped and ringed in the reserve, nine Rufous-cheeked (two males, seven females; Table 2), three Fiery-necked (two males, one female) and one Freckled (female). The brood patch was bare on one male Rufous-cheeked and one male Fiery-necked, while all the females, except Fiery-necked, had a bare brood patch; the body mass of four females suggested that each was carrying a well-developed egg. None ringed in 1988 was retrapped in 1989. Two of the five females fitted with radio transmitters were tracked to nests with eggs; a third shed her transmitter within hours, while the signals from the other two were never heard again after the birds were released.

Behaviour of female F27.—Trapped on 27 September 1988 at 19.15 h, on a road opposite the small dam on the Tetete River at *c*.1,200 m, when released at 21.00 h she flew west. Tracking her signal showed that she then moved south slowly, probably feeding, toward

TABLE 2

Rufous-cheeked Nightjars *Caprimulgus rufigena* trapped, weighed and ringed in Quiet Waters Nature Reserve. M = male, F = female. Some were fitted with radio transmitters (tags) and/or Betalights. Contents of nests 1–5 are shown. c/1, c/2 = clutches of one, two eggs. Neither bird was captured at nest 5.

Ring no.	Ref. No.	Mass (g)	Tag no.	Betalight	Egg size and mass
BB 08327	F27	59	230		Nest 1. c/2, not measured Nest 2. c/1, 28.3 × 20.9 mm; 6.5 g Nest 3. c/1, not measured
BB 08329	F29	60, 61	280		Nest 4. c/2, 26.9 × 20.3 mm, 26.0 × 19.9 mm; clutch mass 10 g
BB 08330	F30	64 (egg?)	310		
BB 08331	F31	66 (egg?)	310		
BB 08332	M32	54, 49	220	Yes	
BB 08335	F35	66 (egg?)			
BB 08336	F36	55	250		
BB 08337	M37	49			
BB 08338	F38	60		Yes	
?	?				Nest 5. c/2, not measured

the boma (livestock enclosure). The following morning, she was roosting, perhaps nesting, on a hill overlooking the upper Tetete River, where it flows into the large dam on Longridge Farm, well outside the reserve. At sunset on 2 October F27 was on the same hillside. For the duration of twilight she moved slowly toward the boma, the fluctuating signal indicating that she was feeding. By 20.00 h, when it was dark, she was back on the hillside, remaining there even after the half-moon rose above Usandisa Kopje at 01.15 h. On 3 October at 15.00 h I got within 20 m of her; she was perched c.20 m below the summit of the tall hill, which has slopes of 30–45° covered in open woodland, with lots of leaf litter, quartz pebbles and some grass. The trees present were small, with an occasional large individual every c.100 m.

With her back to the sun, she crouched with head held lower than most nightjars, giving a hunchbacked appearance. With eyelids closed to slits, she watched me closely, but by moving casually I approached to 2 m behind her. She teetered forward in pre-flight attitude, revealing two eggs aligned parallel to her body. She took off east, circled clockwise, landed 20 m downslope, facing me. This nest ('O1' in Fig. 1) was 1.05 km from where she was captured and 1.45 km from where she was feeding near the boma.

On 4 October at 16.00 h she was sitting facing away from the sun. The eggs, pink in ground colour and evenly marked with large dark freckles, were on a small patch of bare ground. A 10-cm cube of quartz was just below the nest, while a small tree to the west provided afternoon shade. On 11 October at 07.45 h the eggs had disappeared, with no sign of predation or hatching. The last signal for F27 from the nest area was on 9 October at 20.20 h. On 11 October at 16.00 h, she was tracked to the foot of the hill on the west side. Judging by the droppings at the base of a tall tree, she regularly roosted there; no chicks were found in the vicinity.

On 18 October at 05.45 h she was on a single egg at a new nest ('O2' in Fig. 1), on the east side of the hill, c.75 m north-east of, but on the same contour as, the old nest. When checked again at 16.20 h there was still only one egg. On each occasion that she flushed, she flew c.5 m to settle briefly with head up and eyes open, then flew a further 20–30 m.

On the overcast day of 24 October at 11.30 h she was facing downslope into the wind. Her eyelids were narrow slits but on closer approach narrowed even further. There was still only one egg, brownish pink, with lilac and brown blotches and freckles, evenly distributed with a clear patch of 5 mm diameter. The egg's mass was 6.5 g and measurements 28.3 × 20.9 mm. A good signal from F27 came from the nest area on 26 October at 07.00 h.

There was no sign of the female in the vicinity of the nest on 7 November at 16.30 h. Bits of eggshell, with edges nibbled by tooth or bill, suggested predation. On 8 November at 09.10 h F27 was tracked to a new nest ('O3' in Fig. 1), c.100 m north-west of the first, and on approximately the same contour as the first two. She flushed off a single egg and flew north in a series of short (5–10 m) flights until she settled out of sight. At 09.30 h she flew back low over the ground (1 m) to land 5 m from the nest. She was very alert, bobbing her head up and down, eyes wide open. She flipped 2 m nearer, looked around, flipped another 2 m nearer, paused, ran rapidly towards the nest, stopped short of it, paused, then sidled onto the egg without any probing or shuffling. She had her head slightly up, facing downhill with her back to the sun. On 9 November at 08.30 h there was still only one egg.

F27 was still incubating on 13 November at 17.00 h. She returned to the nest at 17.40 h after being flushed, but did not stay long. I remained observing until 19.10 h while the nest was unattended. On 14 November at 17.25 h both female and egg were present. By 19.00 h, when dusk twilight had almost faded, there was no bird at the nest and no eyeshine in the vicinity. At 19.10 h a male called near the nest with three Q-whoop coughs followed by five seconds of churring. I located his eye-shine 1 m west of the nest. The song sequence was repeated five minutes later but he did not return to the nest and was still there at

19.30 h when I left. F27 was in the vicinity of the nest on 15 November at 20.45 h when my observations ended.

Behaviour of female F29.—Trapped 350 m east of the study centre, on 4 October 1988 at 19.30 h, she was released at 20.10 h after being fitted with a radio transmitter. On 9 October at 16.45 h she was tracked to a nest ('O4' in Fig. 1) on the south-west slope of the hill south-east of the study centre, at about the same altitude as the latter. I must have walked past her several times, once within 3 m, without flushing her; only when the Yagi antenna passed over her did she take off, flying 5 m south-east along the contour to settle behind a rock. Two eggs, which scattered 5 cm apart on take-off, were in the same position when I returned at 18.00 h, and the female was still behind the rock.

On 10 October at 16.00 h F29 was on the nest, facing downhill. She flushed east and flew in a semicircle 10 m west of the nest, on the same contour. The nest was <1 m uphill from a narrow game trail, used mainly by Plains Zebras *Equus quagga*. The eggs lay on bare earth surrounded by small angular pebbles of schist and quartzite. A large block of quartzite with a dead branch over it provided some protection one side of the nest. The eggs were less pink, more brown, than those of F27, well freckled throughout, measuring 26.9 × 20.3 mm and 26.0 × 19.9 mm, with a clutch mass of 10 g. On 11 October at 16.40 h she was on the nest. At 18.25 h she flew slowly downhill toward the boma, apparently feeding. She settled at 18.40 h in light rain.

On 17 October at 09.15 h the nest was empty. There were no eggs or eggshells, no chicks or droppings, and no sign of predation. I tracked F29 well down the slope, *c*.200 m due south of the nest. On approach I saw a bird in the shade of a small bush next to a footpath, facing downhill with its back to the sun. It flushed to settle 10 m further on, the bright patches in the plumage identifying it as a male. F29 flushed from 3 m beyond where the male had been; it flew 30–40 m before perching on a low (1 m) branch (2 cm diameter) at the same contour level. No eggs or young were found where either bird had been. At 18.05 h her signal came from where she had settled earlier and for the next 20 minutes she moved steadily west, while male song started nearby. On 18 October at 17.00 h she was at the foot of a large tree on a termitarium 75 m south-east of the nest; sitting on leaf litter but with no eggs. An intermittent signal at 18.25–18.35 h indicated that she was moving downslope towards a small weir south of the boma, with male song coming from the same direction but across the boundary fence.

On 23 October at 17.00 h F29 was roosting 8 m south of a previous roost (see 17 October at 09.15 h), sitting with her back to the sun on leaf litter (no eggs) between two trees providing some shade. She flew horizontally into a strong headwind and tried to perch on a branch 1.5 m high in a small tree, gave up and flew further uphill, turned and glided 30–40 m downwind to settle on the ground east of the roost. On 24 October at 16.30 h she was roosting 100 m west of this position, with her back 45° to the sun on an open patch of pebbly ground (no eggs) with a block of quartzite and thorny shrubs behind her. Acacias a few metres away provided some dappled shade. She flushed *c*.10 m downhill to perch 2.5 m up on a steeply sloping (60°) branch, crosswise back-on. After ten minutes she bobbed her head a few times toward another branch at the same level, 1 m further on, flew there to perch crossways on this 5-mm diameter twig, with her back to me, but head turned. After ten minutes she flew 30 m east to perch 2 m up in the middle of a tree, atop a bow-shaped branch (15–20 mm thick). Seen in bright sunlight, she appeared very grey with dark scapulars and a definite rufous cheek; her posture was upright, with tail at 45°. On 25 October at 18.00 h she was roosting 10 m south-east of the previous day's roost, on a flat stone in dense grass (20 cm high). She again flushed 10 m downhill to perch in a small tree, 2–3 m up, and after two minutes flew to roost on virtually the same spot as the previous day.

On 6 November at 17.00–18.40 h her signal consistently came from beyond the boundary fence south of the boma, in the area where her presumed mate was singing on 18 October. I tracked the transmitter (but no bird) there next morning, on the ground below the fence of a horse paddock, c.0.5 km south-west of the roost area and 1 km from where she was captured.

On 14 November at 20.30 h F29 was retrapped on the road 150 m east of where she had first been captured. All rectrices were intact, so the transmitter had come off cleanly; it was reattached before she was released. On 15 November at 09.00 h she was 100 m south of the usual roost, beside a small tree in a rocky area with large trees. She flew 4 m to settle and watch me (no distraction display) before flying another 30 m; there were no eggs or young where she had flushed.

Behaviour of a pair at the study centre.—On 10 November 1989 at 04.30 h a male was churring near the study centre. Walking along the road toward it, the churring stopped when I was opposite 'O5' (Fig. 1). As I moved away the churring resumed, but stopped again as I returned. A female then flew in with loud *Q!-Q!-Q!* calls and settled on the road 10 m from me, her wings held in a V; each time I walked up to her, she flew up with a *Q*-call to land a few metres further with wings up; this was repeated several times until she had led me well away from the study centre, when she circled round and flew back toward it.

At 20.05 h a male was found on a nest ('O5' in Fig. 1) at the point where the churring had come from earlier, 5 m north of the road among low shrubs. The nest, on bare ground, contained two eggs, dark pink and mottled with numerous darker freckles; the eggs were not handled.

On 11 November at 16.30 h the female was on the nest, facing north-west. She was still there at 18.15 h. She had her back to me, but turned her head 30° to watch me. At 18.37 h she took off silently and flew east; 25 minutes later the male flew in silently from the east, landed directly on the nest and shuffled slightly. Taking a photograph with flash yielded a dramatic reaction; the female appeared almost immediately, uttering *Q*-calls in flight, while the male commenced churring, but remained on the nest. Every flash triggered the same response. The male was on the nest when I left and was still there at 02.00 h, yet at 06.00 h the eggs had gone; no sign of hatching or predation, the only tracks being those of Impala *Aepyceros melampus* 1 m away. Neither bird was captured at the nest, and no new nest was found within their presumed territory.

Description of a nest outside Quiet Waters.—T. Marais showed me colour photographs of a nest found 2 km north of Quiet Waters in November 1980. It was on a rocky outcrop beside a road. Habitat surrounding the nest was mainly rubble, with two tufts of tall grass and several short tufts between rocks 30–40 cm from the nest. Pale buff edges to the outer rectrices of the bird on the nest, with its back to the sun, revealed it to be female. She was incubating two eggs, oriented longitudinally either side of her keel. They were pinkish brown, heavily freckled and mottled throughout, laid on fine gravel with a dozen small quartz pebbles within 5 cm, leaf and grass debris beyond. Two chicks were subsequently seen in the nest, but two days later they had moved 2 m to the foot of the outcrop, on scree of quartzite chips. They were highly cryptic, looking much like small grass tufts, without a definite outline, due to hair-like filoplumes projecting in all directions. Dark transverse bands across crown, back and rump also disrupted the outline. General colour was dark brown and grey, with paler spots, giving them a grizzled appearance. Counter-shading was evident, the buff sides being paler than the dorsal plumage. A whitish W, formed by the eyebrows and two dorsal stripes, provided a further disruptive pattern. Tubular nostrils were prominent on the bill. Blue-grey skin showed on apteria on the rump, lower back and either side of the upper back. Pale feathers encircled the vent.

Behaviour of male M32.—The only male fitted with a radio transmitter was tracked and observed extensively, but never tended a nest. He was not followed when he flew across the boundary fence onto adjoining Longridge Farm. However, radio signals from there indicated he was feeding or passing through. Male M32 was captured on 15 September 1989 at 03.00 h in a mist-net in the study centre car park. Body mass was 54 g and he was fitted with a tail-mounted radio transmitter and a crown-mounted Betalight. He flew off strongly when released.

Roosting.—Radiotracking revealed that M32 spent the daylight roosting on the ground, usually (n = 10) on the north-west slopes of Usandisa Kopje in the north-east corner of the reserve, or (n = 4) c.200–300 m north-west, on adjoining Longridge Farm. A regular roost site ('Oa' in Fig. 1) was located due north-west of Usandisa, just below a footpath on the lower slopes, at c.1,280 m. Despite the radio transmitter signal, it initially took almost one hour to spot him, on an exposed area of sparse leaf litter on a small, flat granite outcrop, which was half below a broken tree on one side and flanked by a tall (1 m) tuft of grass on the other. This provided some shade in the morning. Immediately nearby was a block of quartz, slightly larger than the bird. Numerous droppings showed that he had roosted there frequently; I found him in the same spot on five other days.

When first found, he did not fly until I spotted him, then glided downhill. On subsequent visits, when I did not approach closer than 10 m, my presence did not cause him to flush. He did not assume the hunchback posture often seen during incubation, but adopted the typical nightjar pose, with body flattened and eyes closed to narrow slits. He faced the sunrise but turned his back to the sun for the rest of the day. When it was windy, he faced the wind.

Once he was found roosting on his courtship site ('Ob' in Fig. 1), c.1.7 km south-west of his regular roost. At the time when he would normally have left for the roost at Usandisa, it was dark (the moon set at midnight), overcast (8/8 cloud) and raining heavily. Although the rain gradually eased, these conditions, along with misty mornings, prevailed for three days, during which time he was found at three different roosts on Longridge Farm, c.200–300 m from the regular roost. On the fourth day, after the rain had ceased, he was again at the usual roost.

Roost departure.—I observed the waking sequence once. The first sign of activity was a sideways shake of the head 12 minutes after sunset, and again five minutes later, perhaps attempting to dislodge the Betalight. After two minutes, he raised both wings vertically, while stretching his head and neck forward, then paused before closing his wings, turning and scuttling a few paces to hide behind a tuft of grass. He took off three minutes later, 22 minutes after sunset. M32 left the roost 17–25 minutes after sunset (mean 20.5 ± 2.4, n = 10), towards the end of twilight. However, during the four days of rain, he left the roost significantly earlier ($p < 0.001$), 0–11 minutes after sunset (mean 7.3 ± 5.0, n = 4). The zero value relates to the day he rose at sunset after roosting in the rain at the courtship site. On another occasion, not included above, he left the roost at Usandisa 12 minutes after sunset, when a strong north-east wind was blowing, and flew directly to his courtship site in two minutes. This fast (c.51 km/hour) wind-assisted flight took him over the study centre, where he was seen flying at a height of c.5 m.

Search for a territory.—Early in the season M32 tried to establish a breeding territory in the vicinity of his roost, but the incumbent males prevented him from doing so. When a sound-recording of song was played at the first picnic site below Usandisa (i.e. south-west of M32's roost) on 15 September at 01.00 h, two males arrived almost simultaneously, with repeated *Q*-calls and flying around fast in tandem c.3–5 m above ground. They ranged far and wide for >100 m, flying in formation one above the other, or side by side, with

many *Q*-calls and some *oar!-oar!-oar!* calls. Eventually they settled on the ground 1 m apart to cough (*Q-whoop*) and churr at each other. Singing bouts then occurred at several points around and within the road loop to the south. They continued their churring and formation flights for almost two hours before one bird flew off toward the study centre, while the other, presumably the victor, continued churring at the picnic sites. The presumed vanquished male was trapped in a mist-net at the study centre at 03.00 h; he was ringed and radiotagged as M32.

When the first nightjar song started at dusk on 16 September at 18.15 h, it was M32 churring non-stop for five minutes *c.*150 m west of his roost site, halfway toward the fence. A second male started churring in the vicinity of the picnic sites, followed by a third just across the fence to the north-west. Wedged between these two males, M32 returned to his roost briefly and then (18.20–18.30 h) moved steadily west towards Longridge Dam. He spent much of the night (00.30–03.45 h) on the road opposite the dam north-west of the study centre, sitting quietly or feeding, but at 03.00 h he started churring in earnest, immediately attracting a challenger from the south; this caused him to move further east along the road, accompanied by *Q*-calls from both. The same scenario was repeated several times until 03.45 h, when the two birds performed fast formation flights with *Q*-calls, and much *Q*-whooping and churring on the ground. M32 then flew east, while the other male remained on the road still churring. At 04.00 h M32 was 50 m inside Longridge Farm, across the fence from his roost, singing frequently, on occasions churring non-stop for >5 minutes. He crossed the fence at least twice to sing in the reserve, once accompanied by a second bird.

Establishing a territory.—Subsequent observations in September showed that while M32 often fed on Longridge Farm shortly after leaving the roost, he no longer sang there but moved steadily south-west along the Tetete River towards the small dam and beyond. He spent much of the night, especially moonlit hours, on or near Hayfield B ('Ob' in Fig. 1), in the south-west corner of the reserve. He was present for 49.4–77.7% (mean 62.9 ± 10.1, *n* = 6 nights) of the moonlit period between sunset and sunrise in September, and for 85.3–96.4% (mean 92.9 ± 4.6, *n* = 7 nights) of this period in October. There, *c.*1.7 km south-west of his regular roost at Usandisa, and *c.* 80 m lower in elevation, he defended an area of *c.*3.4 ha.

Fig. 2 shows M32's times of initial arrival on, and final departure from, his territory, in relation to sunset, moonrise, moonset and sunrise. In September, apart from one early arrival, he did not appear on his territory until 0.80–2.25 hours after moonrise (mean 1.63 ± 0.59, *n* = 7 nights), having spent the dark period on Longridge Farm, inactive except for a brief feeding bout at the end of twilight. On 10 October, he was already on his territory at sunset, after roosting there all day; subsequently, he arrived 22–39 minutes after sunset (mean 30.6 ± 6.4, *n* = 8 nights), i.e. after the 22-minute dusk twilight, having fed several times en route from the roost. Final departure from his territory was 19–111 minutes before sunrise (mean 47.7 ± 31.5, *n* = 13), i.e. usually well before dawn twilight. However, during the first half of October, when moonset preceded sunrise, his departure was significantly later (*p* = < 0.01), 17–27 minutes before sunrise (mean 19.4 ± 5.1, *n* = 4), having waited for dawn twilight before leaving.

Song points defining M32's territory.—A bare patch of ground in the hayfield ('Ob' in Fig. 1) was the focus of M32's territory. This small area, *c.*25 m in diameter, is where he spent most of the night, did most of his singing, and attracted most visits by females (Table 3c), so I refer to it as the courtship site ('court'). The major song point within this area was marked by a 6-cm quartzite pebble, which appeared bright in the moonlight. While he particularly favoured this pebble, visiting females appeared more interested in a sandy area around a similar pebble 12 m to the west; so much so that M32 gradually shifted his
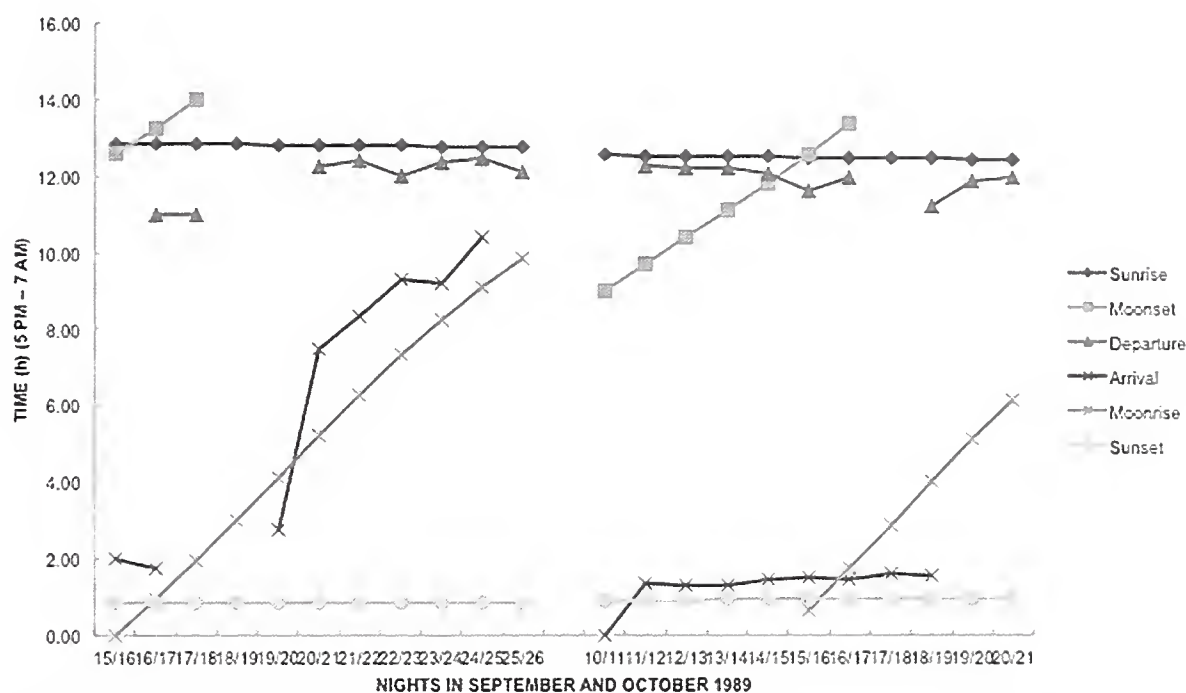
Figure 2. Initial arrival and final departure times of male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) on his court, in relation to sunset, moonrise, moonset and sunrise.

attention there and to a point midway between the two pebbles. A concrete culvert on the north edge of the court provided another regular song point, used frequently when my vehicle was parked too close to the south edge of the court. Mean duration of song at the culvert was greater than at any other point (Table 3c).

The gravel roads and concrete ruins surrounding the hayfield provided several song points used more or less regularly; an inner ring of five, enclosing an area of *c*.3.4 ha (Table 3b), and an outer ring of four, enclosing an area of *c*.17 ha (Table 3a). During my observation periods, M32 visited song points on the outer ring 16 times, those on the inner ring 38 times, and those within the court 125 times (Table 3).

Vocalisations.—A general account of the vocal behaviour of Rufous-cheeked Nightjars, including M32, observed during this study has been published (Jackson 2002d), so here I discuss in more detail the performance by M32 (Table 4). The most-frequently heard vocalisation, and the major activity while in his territory, was the steady churring song, delivered from the ground for up to ten minutes at a time without pause; sometimes, while churring, he faced in a new direction and shuffled sideways. Mean song duration was 82 ± 103 seconds (2–600; *n* = 224); the mean varied from 59 to 90 seconds between song points within the court (Table 3c). There was a noticeable slowing down in churring rate towards the end of a session, thus the finish could often be anticipated.

Churring was mostly heard at dusk and dawn, immediately upon arrival at the court in the evening and intensively again just prior to departure for roost in the morning. During the rest of the night the amount of churring depended mostly on the moonlight available; no moon meant no song, as he did not sing in the dark. The state of the moon also influenced his arrival time and departure from the court (Fig. 2). Once, after leaving the roost, he spent 15–20 minutes feeding on Longridge Farm during twilight, then remained there until moonrise before moving to the court. There was often no activity between the end of twilight and moonrise; even then, sustained churring did not start until the moon was at least 10° above the horizon.

TABLE 3

Number of observed visits paid by a male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) to various song points defining (a) the boundary of his larger territory, (b) the boundary of his smaller territory, and (c) the central court. Visits to these song points by other males or females are indicated by ♂ or ♀ respectively. The location of each song point in relation to the grid lines in Fig. 1 is shown in brackets. Also shown is the mean song duration at each point in the court.

(a) Outer song points enclosing *c*.17 ha

Song point (Ref. in Fig. 1)	Number of observed visits	Direction from court	Neighbour in that direction	Neighbour's song noted (*n*)
Ridge ruins (656/061)	3	N		
Steep Road (655/065)	4 ♂♂	NE	Causeway on road	4
Road at boma (651/061)	2 ♂	S		
Road at west gate (652/057)	7	W		
Totals	16 3 ♂			

(b) Inner song points enclosing *c*.3.4 ha

Song point (Ref. in Fig. 1)	Number of observed visits	Direction from court	Neighbour in that direction	Neighbour's song noted (*n*)
Car park at dam (6535/0605)	14 ♂♂♀	NE	Longridge dam (distant)	3
Road east of dam (653/062)	13 ♂♀	E	Study Centre	1
Road to boma (652/0605)	6 ♂♂	SE	Old claims	8
Concrete floor (6515/060)	3 ♂♂♂	S	Mine dumps (distant)	5
Road to west gate (653/058)	2	W		
Totals	38 8 ♂, 2 ♀			

(c) Song points within the *c*.25-m diameter court

Song point	Number of observed visits	Direction from court centre	Duration of song (s) mean ± SD	Range (s) and number
Culvert	27 ♀	N	90 ± 105	(3–480) 66
East pebble	45 ♂♂♂♀	E	77 ± 100	(2–480) 46
Midway	18 ♂♀♀♀	S	59 ± 80	(2–300) 20
West pebble	19 ♂♀♀♀♀♀♀♀♀	W	80 ± 112	(5–420) 20
Other	16 ♂♂♀♀	random	75 ± 87	(2–330) 67
Totals	125 7 ♂, 16 ♀			

Cloud cover, cold, wind, mist and rain all inhibited song. On several occasions M32 stopped churring as a cloud obscured the moon, then re-started immediately after the cloud had passed. On other occasions, when there was extensive cloud cover, he started singing each time a break permitted moonlight to shine through. Surprisingly, a bright moon overhead on a clear night also appeared to inhibit churring, as if there was too much light. When it was cold and windy M32 faced the wind, huddled up; on a particularly cold night he appeared to leave the valley for higher ground, his radio signal coming from the ridge above the small dam. A noticeable drop in temperature usually resulted in diminished activity. Mist and rain also inhibited churring by M32; once, heavy rain prevented him from leaving the court for his roost, so he spent the day there.

Churring was usually preceded by a few preliminary coughs, with slight pauses, e.g. *Q-whoop ... Q-whoop ...Q-whoop ...* churring. The bird had its head down and tucked in while uttering the coughs, then stretched forward head up while churring, prominently exposing the white throat patches. My impression was that the preliminary coughs were a means of gulping air into a reservoir, to fuel the churring; however, the duration of churring did not seem dependent on the number of coughs. Sometimes (15%) churring started without any preliminary coughs. Emphasis in the cough was on the first element, which is a less explosive version of the *Q*-call. As many as nine preliminary coughs were noted, but mean was 4.3 ± 2.2 (1–9; $n = 140$).

The steady churring song of M32 changed tone in response to the arrival of another male or a female. Males were greeted with a continuous series of much louder, harsher *oaroaroar* notes, while females provoked a continuous series of more mellow, purring notes. A change in tone alerted the observer to the arrival of another bird. M32 occasionally appeared to mistake the sex of the visitor, so that churring turned to purring to oaring in a single continuum. The oaring and purring are simple variations on the territorial song, each being uttered as a continuation of, and at the same rate as, the churring.

These vocalisations were all performed while M32 was on the ground; in-flight vocalisations comprised two distinct calls, an explosive, staccato *Q!-Q!-Q!* and a guttural *oar!-oar!-oar!* *Q*-calls were frequently heard during feeding flights, mainly on take-off, occasionally on landing, and often during formation flights with a female. *Oar*-calls, as many as 30, with some *Q*-calls interspersed, were heard mostly during aerial skirmishes with other males. Subjectively, the *Q*-call sounds excited, the *Oar*-call aggressive. The former is a scaled up version of the first element in the preliminary cough (*Q-whoop*), while the latter is derived from oaring by breaking up the continuous *oaroaroar* series into separate *oar!-oar!-oar!* notes.

Reaction to intruders.—The largest intruder into M32's territory was the vehicle used as a mobile hide; this was normally parked, prior to his arrival at dusk, on the south edge of the court and facing, at a distance of 10–15 m, the two pebbles used as song points. Switching on parking lights triggered a churring response, while dimmed headlights caused him to move to sing elsewhere on the court, so virtually all observations were made in moonlight alone. Once, when caught in the beam of a headlight at *c.*3 m, he turned sideways through 180° a few times, broadside on, then faced the light, put his head down as if to peck the ground, and flew off.

M32 responded to movements and sounds from the vehicle, such as the radiotracking *kips* made by the receiver, by flying straight towards the cab with repeated *Oar*-calls before returning to his song point. The vehicle's proximity seemed to cause him to spend less time singing near the east pebble, his favourite song point, and more time 20 m north on the culvert song point, where mean song duration was greatest (Table 3c). The mean for the court as a whole, with the vehicle present, was 89 ± 104 seconds (2–480; $n = 165$). To

check whether the vehicle inhibited singing, I parked behind a tree on the boma road, 85 m from the court, from dusk to midnight on 15 October. Contrary to expectation, mean song duration decreased to 46 ± 60 seconds (2–270; $n = 54$).

Several times, when viewed through binoculars, M32 deliberately hid from view behind a tuft of grass, remaining absolutely still for some time before flying directly towards the cab with Q- and Oar-calls. The bird was clearly aware of me, especially during bright moonlight, despite screening the windows. He was also aware of ungulate activity at the west of the hayfield, where cattle and wild game congregated at the Duncan Applicator, which provided tick control. Whenever a commotion occurred, M32 flew over the animals uttering many Q- and Oar-calls, before returning to his song post. The bare court was created by the hooves of these ungulates, while the applicator was at the east end of the hayfield.

Greater Kudus *Tragelaphus strepsiceros*, up to ten but usually <5, often crossed his court, sometimes browsing on the trees next to the culvert song point. They seldom caused him to fly, but he stopped singing, although he occasionally gave some preliminary coughs without churring, only resuming when they left. He crouched down in cryptic posture, even when some kudus passed as close as 1 m. Once, while churring from the normal tarsus squat, he swung round to face a kudu approaching 10 m away, rose onto his toes and churred at it strongly, behaviour repeated towards a rival male nightjar on another occasion.

When a group of Bushpigs *Potamochoerus larvatus* spent 30 minutes in the north-east corner of the hayfield, squealing loudly, M32 continued churring with lengthy songs on at least ten occasions. He also continued churring for 84 seconds despite the raucous song of a Water Thick-knee *Burhinus vermiculatus* a short distance away. A Scrub Hare *Lepus saxatilis* approaching the east pebble caused him to spin round to face it, before flying up to land 2 m beyond it, without any Q- or Oar-calls; facing the hare, he continued feeding with short flights into the air. On separate occasions, while M32 was away, a Side-striped Jackal *Canis adustus* and a Serval *Leptailurus serval* (both potential predators) crossed his court.

Reaction to conspecifics.—When a Rufous-cheeked Nightjar was heard singing in the distance, M32 faced that direction and churred steadily. However, song anywhere within his territory caused him to immediately fly towards it, giving Q-calls. Three times, while M32 was absent, an intruder flew to the court, sat for a while, coughed a few times and churred. The radio signal immediately revealed that M32 was returning, with Q-calls being heard. Both then flew around in formation, with many Q-calls, before the intruder left and M32 returned to the court to churr for several minutes; once, however, the two birds first hopped around each other, flipping towards each other, before taking off. M32 took no notice of Fiery-necked and Freckled Nightjars—whistlers not churrers—that regularly sang in his territory.

Conspecifics flying silently over the court triggered a steady churring from M32, apparently serving as both a warning to males and invitation to females; when close enough to identify, his churring changed to loud oaring if it was a male, or to subdued purring for a female (Table 4). A nightjar landing on his court immediately provoked M32 to take off with Q-calls, fly at the intruder, quite often over it, and land nearby with wings in a dihedral V, the white bars being conspicuous. Subsequent behaviour depended on the response of the intruder. Males usually took off with Q-calls and flew away, in which case M32 followed, also with Q-calls, to evict them from his territory, before returning to sing on his court. However, twice the intruder flipped towards M32 with Q-calls, both birds then repeatedly flipping at each other while calling, before taking off.

Females on the court seldom moved towards M32 if he was wearing the radio transmitter, but often ran or flew toward him when he was wearing the crown-mounted

TABLE 4

Vocalisations uttered by a male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) and the context in which they occurred. No recordings were made of these vocalisations, so no sonograms are available.

Vocalisation	Sound	Description	Context
Preliminary coughing	*Q-whoop … Q-whoop … Q-whoop …* with slight pauses between coughs.	Like kick-starting a vintage motorcycle a few times before it fires. Emphasis on the first syllable. Terrestrial only.	Churring song is usually (but not always) preceded by some of these coughs.
Churring	*RRRRRRRRRRRR…* continuous.	Like the steady, rather high-pitched firing of a two-stroke engine. Terrestrial only.	Proclaimed from song points defining M32's territory, especially in the court, to warn off males and attract females.
Oaring	*oaroaroaroaroaroar…* continuous.	A louder, more guttural version of churring song. Terrestrial only.	Churring songs usually ended in oaring when a male arrived in the vicinity of M32.
Purring	*rrrrrrrrrrrrrrrrrrrrrrrrr…* continuous.	Subdued form of churring song, at a lower pitch. Terrestrial only.	Churring songs usually ended in purring when a female arrived in the vicinity of M32.
Q-call	*Q!-Q!-Q!-Q!* … staccato with very slight pauses between calls.	A more explosive form of the first syllable (*Q-*) in the preliminary call. Like striking a metal pipe with a wooden stick. Mainly aerial but also terrestrial.	An excited call given during feeding flights; during formation flights with other males in territory defence, and courtship flights with females.
Oar-call	*oar!-oar!-oar!-oar!* … with very slight pauses between calls.	Similar to oaring, but with individual, rather than continuous notes. Mainly aerial but also terrestrial.	Aggressive call given on take-off or after landing. Often interspersed with Q-calls in flight.
Protesting	Rasping hissing	A low, hoarse, rasping, growling hiss. In-hand only.	Whenever handled, M32 gaped widely and repeatedly uttered this protest.

Betalight. With this exception, the behaviour of females, and of M32, appeared identical whether he was wearing the transmitter or the Betalight alone. A female usually sat quietly when M32 landed next to her, then walked or ran around, as if looking for a suitable nest site, sometimes shuffling or turning around on the spot, while M32 sat quietly watching her, occasionally flipping nearer. Each flip started with a Q-call and ended with a wings-up landing. She was quiet but he occasionally coughed and churred briefly between flips. During an extended walkabout by a female, M32 flew around her, making Q-calls, landed some metres away and started churring. Often, the female ran or flew to him. At times, they performed an 'advance and retreat' display, by hopping around or flipping to and fro with Q-calls. Whenever he landed right behind her, she spun round to face him.

Copulation was never observed and no nest was found on or near the court. All female visits ended with her flying away, usually (12/16) followed by M32, with both giving Q-calls. He (10/12) returned to the court within 20 minutes to resume churring. Once it was the female who returned, after 13 minutes, with M32 following. On another occasion, he was accompanied by a new female (F38) as he flew in from the east at dusk, heading for the court; they were flying in formation, 3 m apart, when they were both caught in a mist-net next to the culvert M32 used as a song point (Table 3c). She was not radio-tagged but a Betalight was glued to her crown; while being handled she gave a number of quiet *oar-oar-oar* notes and, when my fingers approached her crown, she gaped upward and hissed. She

weighed 60 g prior to voiding a huge dropping, so had already fed. Released at 19.45 h, she sat for two minutes, turning her head slowly sideways, then shaking it horizontally, trying to dislodge the Betalight. She ran a few steps, stopped and shook her head again; after repeating this several times over a distance of 3 m, she took off silently towards the main gate. She did not attempt to remove the Betalight with her foot. At 21.13 h she was seen near the main gate, with the Betalight still in place. She was not seen again. It is unlikely that they were paired; while her brood patch was devoid of feathers, his was not. Also, during his absences from the court at night, radiotracking showed him to be feeding elsewhere, not attending a nest.

Feeding.—After leaving the roost in the evening, M32 spent much of the dusk twilight (22 minutes) feeding, either on Longridge Farm or en route to his court. Once there, the main activity was singing, but his head movements suggested that he kept constant watch for passing insects. When spotting one flying over, he took off with *Q*-calls to catch it, sometimes with an audible snap of the bill, before gliding back to the same spot, often with another *Q*-call, then immediately resumed churring. At times he left the court to feed near the small dam, his favoured observation platform being the adjoining road to the east, next to some thorn trees.

Feeding flights, up to 25 in five minutes, seldom (<50%) reached a height of >1 m, and did not exceed 5 m. Most flights were simply out and back, but a few involved aerobatics in a figure eight, with sharp twists and turns. On landing he sometimes ran a few steps, and occasionally he bent over hunched as if processing prey, but he was not seen chasing insects on the ground. When first trapped, on 15 September at 03.00 h, M32's body mass was 54 g. When recaptured, on 18 October at 18.35 h, it was only 49 g, with stomach *c*.25% full.

Resting and preening.—There were many periods of inactivity during the night, when M32 did little feeding or singing, especially if there was no moon, or it was cloudy, cold or windy. He sat quietly, without moving, for 30 minutes or more at times. This usually coincided with a general lack of nightjar activity anywhere in Quiet Waters. It was during these periods that he occasionally preened, an activity observed just eight times and never involving the flight feathers. He concentrated on the ventral plumage, mainly on the breast and belly.

Discussion

Comprehensive summaries of published data for Rufous-cheeked Nightjars are presented in two monographs of the Caprimulgiformes (Cleere 1998, Holyoak 2001) and in *Roberts VII* (Spottiswoode & Jackson 2005). Much of what was discovered during the Quiet Waters study confirms the information in these summaries, but some new observations require discussion.

Lunar effects.—All nightjar species at Quiet Waters were active mainly during the twilight periods. Nocturnal activity was observed only when sufficient moonlight was available; the brighter the moon, the more activity; with no moon, there was no singing or feeding; the birds just sat quietly. Even a temporary reduction in moonlight inhibited activity temporarily, as when M32 ceased churring as a cloud obscured the moon, only to resume immediately it passed. Shaw (1998) observed avian behaviour during a total lunar eclipse, noting that a Square-tailed Nightjar that had been singing fell silent during it, not singing again until half the moon face was exposed.

Several nightjar species synchronise breeding with the lunar cycle (Holyoak 2001). In Africa Fiery-necked, Freckled, Square-tailed and Pennant-winged Nightjars lay during the week following full moon (Jackson 1985), but this has not been demonstrated for Rufous-cheeked Nightjar. The full-moon dates relevant to the nests in this study were 25 September

and 24 October 1988, 14 October and 12 November 1989. The incubation period being 15–17 days (Fry & Harwin 1988), it is probable that the eggs found on 3 October 1988 (F27) and 9 October 1988 (F29) were laid during the week following the 25 September full moon, but it is also possible that F29 did not lay until the second week after full moon. Neither of the two replacement clutches laid by F27 could have been laid during the first week after the 24 October full moon; the first was found on 18 October and the second, found on 8 November, was still there on 15th. The nest at the study centre already had eggs two days prior to the 12 November full moon. Replacement clutches and late nests are less likely to be synchronised with the lunar cycle, so the early clutches laid by F27 and F29 provide the best evidence that Rufous-cheeked Nightjars also synchronise their breeding with the lunar cycle. Further research is required to confirm this. With regard to their closest relatives, Perrins & Crick (1996) showed that European Nightjars that arrive relatively early on the breeding grounds (i.e. in May) appear to start nesting as soon as possible, but the rest, which initiate nesting between early and mid June, tend to synchronise nesting with the lunar cycle.

Jetz *et al.* (2003) studied the effects of light and prey availability on nocturnal, lunar and seasonal activity in West Africa of Long-tailed Nightjar *C. climacurus* and Standard-winged Nightjar *M. longipennis*. They demonstrated the distinct nocturnal, lunar and seasonal pattern of both light availability and aerial insect biomass, and highlighted the significance of moonlight above and beyond prey availability. They demonstrated that the lunar cycle affects short-term timing of foraging activity and breeding, while prey biomass, modulated by patterns of rainfall, governs presence and seasonality of breeding. Nocturnal foraging was positively correlated with lunar light levels and ceased below *c.*0.03 mW m^{-2}. White-winged Nightjar *Eleothreptus candicans* nesting attempts in Paraguay exhibited remarkable synchrony with the full moon; the first egg was laid within two days of full moon for all seven clutches where laying date was confirmed (Pople 2014).

Nests, eggs and young.—Crypsis is a recurrent theme in the lifecycle of all nightjars. The superb camouflage provided by the cryptically coloured plumage, which has evolved to blend perfectly with the preferred substrate, protects the adult both at roost and while on the nest. The counter-shading, disruptive pattern and hair-like filoplumes of the downy chicks make them extremely difficult to see (Uys 1984, Steyn 1996), especially when they are immobile. Even the eggs are cryptically coloured, as noted for this species by Hoesch & Niethammer (1940). The eggs are laid directly onto the substrate, so the nest is invisible. With no nest structure to direct attention to the site, how do the owners find it? I suggest that they use the quartzite blocks often found near the nest for navigation. The behaviour of M32, using a quartzite pebble as a song point, supports this suggestion, as does the block of quartz at his roost, and those at many roosts of F29.

Carlyon (2011) noted that when Rufous-cheeked Nightjars select a nest site, moist areas are avoided, with elevated sites such as hillsides or ridges being preferred. Each of the six nests in the Quiet Waters area was near the summit of a hill or on a ridge. That none of the females visiting M32's court accepted the site for nesting may have been due to its low-lying, rather moist situation. As in some other nightjars (Jackson 1985), females incubated the eggs by day, males at night. Males occasionally sit during the day, e.g. one photographed at Olifantsfontein by W. Tarboton (*in litt.* 1969) and a Fiery-necked Nightjar captured on Ranelia Farm, Chipinga (Jackson 1985).

Double-brooding by Rufous-cheeked Nightjars has never been recorded, and neither have replacement clutches, so it is significant that F27 laid two successive replacement clutches. In contrast, F29 did not lay a replacement clutch after her eggs disappeared in mid October, well before the end of the breeding season; radiotracking revealed that she and her mate remained in his territory, but had not moved her eggs to a new location (*cf.* Jackson

2007 for a discussion of nightjar nest translocation). While F27's behaviour shows that the birds sometimes replace lost clutches, it also suggests that some females raise two broods in a season. Clutch size is 1–2 (Cleere 1998), but single-egg clutches are rare (Holyoak 2001), <3% (Spottiswoode & Jackson 2005). They may well be commoner in replacement clutches, as the only single-egg clutches found in this study were the two replacement clutches laid by F27.

Territory, monogamy and fidelity.—This study confirms that Rufous-cheeked Nightjar is a solitary, monogamous breeder and that males defend a territory during the breeding season. Ownership is proclaimed and territory defined by churring from terrestrial song points around and within the area. Females attracted by the singing inspect potential nest sites within the territory and once one of them accepts a nest site, breeding may commence. As noticed by Carlyon (2011), while males sing frequently within their territories, they become silent once breeding has commenced. Breeding males in this study sang briefly at dusk as they assumed incubation from the females; singing while on the nest could attract the attention of predators. The inordinate amount of singing by M32 suggested he was a bachelor, especially as radiotracking failed to lead to a nest.

Because only half of the 220-ha reserve provided suitable breeding habitat for this species, the mean size of the six territories identified could have been no more than c.18 ha. The outer song points used by M32 enclosed c.17 ha (Table 3a), but these were visited only 16 times, compared to 38 visits to the inner points, which enclosed c.3.4 ha (Table 3b), and 125 visits to those within the c.25-m diameter court (Table 3c). These results, which beg the question as to what constitutes the territory, show that territory defence is strongest in a small central display area (court), gradually diminishing outwards. White-winged Nightjars in eastern Paraguay also have a small display arena at the centre of a much larger territory (Pople 2014).

Birds were found roosting or feeding well outside their territories. M32 regularly roosted 1.7 km from his court, and frequently foraged in rival territories while en route between roost and court. F27 was captured 1.05 km from her nest, and was subsequently seen foraging 1.45 km from it. R. Earlé (*in litt.* 1988), while radiotracking Square-tailed Nightjars in Kruger National Park, South Africa, found that one travelled >3 km between its roost site and foraging area at dusk. Radio-tagged European Nightjars in Dorset travelled a mean 3.1 km from their nesting areas at night to atypical habitats, presumably to feed (Alexander & Cresswell 1990).

None of the birds captured in 1988 was recaptured in 1989, so my data provide no information on site or mate fidelity. However, breeders in the Transvaal were recaptured in three successive years (Tarboton *et al.* 1987), demonstrating site fidelity, perhaps even mate fidelity. Another, ringed in Nylsvlei Nature Reserve, and recaptured in exactly the same area 14 months later, suggested to van Eeden (2005) that this intra-African migrant returns to breed in a preferred area each year.

Vocalisation and wing-clapping.—The male's basic song is a prolonged steady churring at between 31 notes/second (Walker 1969) and 32–37.5 notes/second (Fry 1988). One Quiet Waters male, timed by stopwatch, churred without pause for 20 minutes, eight seconds (Jackson 2002d), a performance of 37,448–45,300 notes! Churring tends to slow towards the end of a sustained singing session, but not to the extent that Fry & Harwin (1988) claim, repeated by Cleere (1998) and Holyoak (2001); the series of slower, lower-pitched units, *wha wha wha wha wha wha wha wha* that they describe is unlike anything heard at Quiet Waters (Table 4), but is similar to the monotonous wooting call of Fiery-necked Nightjar, often heard there (Jackson 2002d); clearly a case of mistaken identity. The churring song serves to proclaim the territory to other males, and probably invites females to breed.

Any conspecific visitor is greeted with oaring, in the case of a male, or purring, for a female (Table 4). The deimatic oaring and epigamic purring are variations on the territorial song, each being uttered as a continuation of, and at the same rate as, the churring.

Two distinct flight calls are heard; an excited staccato *Q!-Q!-Q!-Q!* … with very slight pauses, and an aggressive *oar!-oar!-oar!-oar!* … also with very slight pauses. The former is a more explosive version of the first element in the preliminary coughs (*Q-whoop* … *Q-whoop* … *Q-whoop* …) usually given prior to churring, while the latter is derived from oaring song. Ranft & Cleere (1998) provided a sound-recording that includes several preliminary coughs, sustained churring and a few Q-calls. Sonograms in Fry (1988), sound-recordings in Chappuis (1981) and the FitzPatrick Bird Communications Library, depict the preliminary cough and sustained churring of a Rufous-cheeked Nightjar. None of the sonograms that I have seen, or recordings that I have heard, has captured either the oaring or purring extension to the song.

According to Cleere (1998) males clap their wings in flight during courtship displays, or when pursuing males that enter their territory. This behaviour was not observed during 375 hours of observation at Quiet Waters. Wing-clapping was observed just once, in a different context, when a male taking off from a 7–8 m-high tree gave two explosive wing-claps (Jackson 2002d). Wing-clapping is common in European Nightjars, mainly by males in aggressive contexts, courtship display and even on take-off when flushed from the ground (Holyoak 2001), but is uncommon in Rufous-cheeked Nightjar, despite their close relationship.

Courtship and breeding status of male M32.—Interested females responded to the churring song of M32 by flying into his court and landing nearby. As she approached, his churring changed to purring and he flew towards her with Q-calls, landing with his wings in a dihedral V (displaying the white wingbars) before folding them. Initially the female sat still before searching for a suitable nest site, even turning around and shuffling sideways to get the feel of it. M32 sat watching her, singing occasionally and performing short horizontal flips. Some females left at this stage, flying off with M32 in pursuit, both giving Q-calls. Others responded by approaching and interacting with him in an 'advance and retreat' display, each bird performing short vertical hops and flips. None of these displays culminated in copulation; whenever M32 landed behind a female, she spun round to face him.

The reason M32 failed to secure a mate could be due to one or more factors, the most obvious being that during courtship encounters he was wearing either a radio transmitter or a Betalight. Females appeared to be attracted by the Betalight, as they flew or ran towards M32 more often when he was wearing it; perhaps they were simply curious about this unusual glow in the semi-dark. As European Nightjars wearing identical transmitters and Betalights bred and foraged normally (Cresswell 1985), it is unlikely that those on M32 inhibited courtship or copulation.

On 15 September, M32 weighed 54 g, but on 18 October only 49 g. This loss of mass was thought to be due either to the energy lost during the enormous amount of singing that he did, or due to the radio transmitter and/or Betalight he was carrying during this period (33 days). However, another male (M37), not wearing either, and caught in the same mist-net as M32 a few minutes earlier, also weighed 49 g. Palpation showed that both their stomachs were virtually empty in the early evening, so M32 may well have had a full stomach on 15 September at 03.00 h, but it was unfortunately not palpated. Since his brood patch was feathered, he may have been an inexperienced first-year, less likely to attract a mate.

The most likely reason for his lack of success, however, was the unsuitability of his territory, especially the moist, low-lying courtship area, for nesting. Observations of

courtship by a pair of Rufous-cheeked Nightjars in South Africa (Tyler 1992) showed behaviour very similar to that observed in this study, suggesting that M32 was behaving in a manner representative of the species. Females were attracted and interacted with him, but rejected his territory, which he occupied only after challenging unsuccessfully for more suitable territories uphill in the vicinity of his roost.

Superspecies comparisons.—European, Rufous-cheeked and Sombre Nightjars C. *fraenatus* form a superspecies (Fry 1988). The behaviour of Rufous-cheeked, as displayed by M32, can be expected to be similar to that of its two allospecies. While little has been published on the behaviour of Sombre Nightjar, the literature on European Nightjar is extensive. European Nightjar is a trans-continental migrant, Rufous-cheeked Nightjar a trans-equatorial migrant and Sombre Nightjar mainly resident, with local movements according to the state of the vegetation (Holyoak 2001).

As discussed by Holyoak (2001), Sombre Nightjar is variously believed to be a whistler (Dowsett & Dowsett-Lemaire 1993) or a churrer (Cleere 1998). Afrotropical *Caprimulgus* have adapted both their songs and degree of p9 emargination to their habitat; the whistlers, which have stronger emargination, occur in more closed habitats, while the churrers, which have weaker emargination, occur in more open areas (Jackson 2002d). Sombre Nightjar, which occurs in open habitats (Holyoak 2001), was placed in the churring group on the basis of its weak p9 emargination (Jackson 2002b). A sound-recording of the churring song (Ranft & Cleere 1998) is extremely similar to Rufous-cheeked Nightjar (Cleere 1998), even ending in three *Oar*-calls. The recording of a European Nightjar's churring differs from both in constant changes of speed and pitch, alternating between a faster, lower pitched churr and a slower, higher pitched one, in much the same way that Square-tailed Nightjar song does.

Comparing the territorial and breeding behaviour of European Nightjars (Holyoak 2001) with Rufous-cheeked Nightjar (this study), there are many similarities in territory establishment, size and defence, but the latter performs much less wing-clapping and less volplaning with wings in a V, seldom sings from arboreal perches and does not roost there. Both species are monogamous (Sombre Nightjar too, probably), with adults sharing nest duties, but while in Afrotropical species the female attends by day and male at night, in European Nightjar, which has evolved overlapping broods in response to the short Palearctic summer, females incubate the second clutch day and night, while males tend the first brood night and day (Jackson 1985). European and Sombre Nightjars feed mainly in sustained flight (Holyoak 2001), while Rufous-cheeked Nightjar forages mostly by short sallies from a terrestrial perch (this study).

Radiotracking and Betalights.—A primary purpose of my study was to test the effectiveness of radiotracking and Betalights as aids for studying nightjars. Despite some limitations, radiotracking proved an invaluable tool. Without radiotracking, the roost site of M32 and the nests of most females would not have been found. The Betalight was helpful while observing courtship, feeding or preening, but I recommend that it be mounted on the radio transmitter body or antenna, as shown in Hayward (1987), rather than on the nightjar's crown.

Conclusion

The shortcomings of this study are obvious; too few observers ($n = 1$), too few observer nights/hours ($n = 49/375$), too few radio transmitters ($n = 5$), too few study individuals (*c*.12), small sample sizes, no night-vision binoculars, no sensitive light meter, no tape-recorder and no GPS. Despite these limitations, new insights were obtained into the breeding-season

behaviour of Rufous-cheeked Nightjar, especially its roosting, territory establishment and defence, vocalisations, courtship, nesting and feeding.

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A new species of extinct *Pterodroma* petrel (Procellariiformes: Procellariidae) from the Chatham Islands, New Zealand

by Alan J. D. Tennyson, Joanne H. Cooper & Lara D. Shepherd

SUMMARY.—A new species of extinct gadfly petrel (Procellariidae, *Pterodroma*) is described from the Chatham Islands, New Zealand. Its remains have been recovered in Holocene fossil deposits on Chatham, Pitt and Mangere Islands. Its extinction, possibly as late as the 19th century, was a result of human colonisation of the island group. The new species was identified by a combination of morphological and molecular evidence. A complete humerus was selected as the holotype by soaking DNA from the fossil bone, leaving its morphology intact.

Cooper & Tennyson (2008) suggested that an undescribed extinct Holocene species of gadfly petrel (*Pterodroma* sp., Procellariiformes, Procellariidae) occurred on the Chatham Islands (44°S, 176°W), New Zealand. They used max. post-cranial bone lengths to identify isolated elements that probably belonged to an undescribed species, which they referred to as '*Pterodroma* sp. 1'. In size, this taxon fell between the range of the known *Pterodroma* species that breed on the Chatham Islands today: it was smaller than Magenta Petrel *P. magentae* (Giglioli & Salvadori, 1869) and larger than Chatham Petrel *P. axillaris* (Salvin, 1893) and Black-winged Petrel *P. nigripennis* (Rothschild, 1891). However, they were unable to assign with absolute certainty any bone to *Pterodroma* sp. 1 because many species in the diverse large genus *Pterodroma* have morphologically very similar skeletons, and the quality of the available specimens was too poor (i.e. they were incomplete, and/or were represented almost entirely by isolated elements only) and no cranial material was available to enable full comparisons.

The existence of an extinct, possibly undescribed, medium-sized *Pterodroma* petrel at the Chatham Islands has previously been suggested by several authors (e.g. Bourne 1967, Tennyson & Millener 1994, Holdaway *et al.* 2001). Also, possible relationships between this extinct taxon and Murphy's Petrel *P. ultima* Murphy, 1949 (see Bourne 1967) or Mottled Petrel *P. inexpectata* (J. R. Forster, 1844) (see Millener 1999, Worthy & Holdaway 2002) have been proposed. In size, however, this taxon is closer to Soft-plumaged Petrel *P. mollis* (Gould, 1844) (Cooper & Tennyson 2008).

We used molecular techniques to clarify the identity of this Chatham Island bird, whose bones were considered by Cooper & Tennyson (2008) to be an undescribed species. In addition, we present an extraction technique to isolate DNA from bones, which not only reduces physical damage to a minimum but, also, permitted us to identify a suitable specimen as the holotype of the new species described herein.

Methods

Specimens examined and used for DNA extraction are all deposited in the collection of the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (Te Papa) (NMNZ).

The sequence and nomenclature of taxa follow Dickinson & Remsen (2013), with the exception of Kerguelen Petrel *Lugensa brevirostris* (Lesson, 1833) and White-naped Petrel *P. cervicalis* (Salvin, 1891), whose nomenclature follows Gill *et al.* (2010).

All DNA extractions and polymerase chain reaction (PCR) set-ups were performed in a dedicated ancient DNA (aDNA) laboratory physically isolated from where modern DNA and PCR products were handled. Potential contamination was monitored by the use of negative extraction and PCR controls.

Approximately 5 mm from the broken ends of three humeri (NMNZ S.27584.1, S.37589.1, S.37589.2 examined by Cooper & Tennyson (2008) and considered by them to belong to species *Pterodroma* sp. 1) were removed using a Dremel grinder with a new Dremel wheel used for each bone. Each sample was powdered by grinding in a sterilised mortar and pestle. Bone powder was then decalcified and a phenol-chloroform extraction performed (Shepherd & Lambert 2008).

Additionally, an alternative method using a Qiagen DNeasy Blood and Tissue kit was used for DNA extraction from eight relatively undamaged humeri (NMNZ S.29601.1, S.30019, S.30985.1, S.31531.1, S.31633, S.32287, S.35342.1, S.37622.1) considered by Cooper & Tennyson (2008) to belong to the same taxon. With this method, we aimed to extract aDNA without damaging the gross morphology of the bones. The method is modified from extraction methods for powdered bone described by Rohland & Hofreiter (2007a,b) but uses a commercial kit and is much quicker. The distal end of each bone was soaked in 2 ml of 0.5M EDTA, 40 µl SDS and 30 µl 50 mg/ml proteinase-K for six hours. The first five humeri that we soaked were heated to 55°C with a heating block but this caused a small amount of surface bone to dissolve. For the subsequent three bones we reduced the temperature to 45°C and were able to eliminate almost any morphological damage. This solution was then added to 2 ml AL Buffer (Qiagen) and incubated for ten minutes, 2 ml of 100% EtOH was added and the resulting solution centrifuged through a Qiagen DNeasy column. The extraction was completed by washing with the kit's buffers, following the manufacturer's instructions, and eluting in a final volume of 50 µl of Buffer AE. Following the extraction, the bones were soaked in distilled water for eight hours, then allowed to dry at room temperature.

The collection locations, collection dates, collectors and former identities of the sampled bones are shown in Table 1. Humeri were selected for sampling because they are relatively large bones and were the most common of the elements preserved of the putative new taxon (Cooper & Tennyson 2008).

We used multiple Soft-plumaged Petrel samples for our comparisons because of the similarity in size between this species and '*Pterodroma* sp. 1' (Cooper & Tennyson 2008). DNA from footpads of four Soft-plumaged Petrel study skin specimens (NMNZ OR.22888 Macquarie Island, OR.23060 Kerguelen Island, OR.25195 New Zealand beach, OR.26227 Antipodes Island) was extracted using a Qiagen DNeasy Blood and Tissue kit, following the manufacturer's instructions.

For PCR amplification of DNA extracted from the broken bones, we targeted short overlapping fragments of two mitochondrial DNA loci. Although it would be ideal to analyse sequences from multiple independent nuclear loci, rather than relying on a single locus, such data are presently not available for the majority of petrels. Primer pairs from Patel *et al.* (2010) were used to amplify fragments of the cytochrome *c* oxidase (CO1) locus from *Pterodroma* sp. 1 and Soft-plumaged Petrel. Fragments of cytochrome *b* were amplified for *Pterodroma* sp. 1 using the primers from Brace *et al.* (2014).

For PCR amplification of the soaked bones, novel primers (shortPBF: TCGCCCTACACTTCCTCCTA and shortPBR: GATTTTGTCGCAGTTTGATACGA) were

TABLE 1

Sampled *Pterodroma* bones from the Chatham Islands, including collection locations, collection dates, collectors, and former identities. The former identities were mostly by P. R. Millener, but bones collected by R. Richards & AJDT were identified by AJDT. All were subsequently re-identified as '*Pterodroma* sp. 1' by Cooper & Tennyson (2008).

NMNZ reg. no.	Locality	Date and collector	Original identifications
S.27584.1	Pitt I.	1947, C. Jefferson	'*Pterodroma*' and '*Pterodroma* cf. *inexpectata*'
S.29601.1	Okawa dunes, Chatham I.	21 Feb 1991, P. R. Millener	'*Pterodroma*' and '*Pterodroma* > *inexpectata*'
S.30019	Long Beach, Chatham I.	2 Mar 1991, P. R. Millener	'*Pterodroma* ?'
S.30985.1	Maunganui Beach, Chatham I.	2 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.31531.1	North Head, Pitt I.	8 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.31633	Te Ana a Moe, Chatham I.	10 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.32287	Long Beach, Chatham I.	16 Feb 1991, P. R. Millener & N. Hyde	'*Pterodroma inexpectata*'
S.35342.1	Waipawa Mouth, Pitt I.	27 Feb 1992, R. Richards	'*Pterodroma* cf. *inexpectata*'
S.37589.1	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'
S.37589.2	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'
S.37622.1	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'

designed to target a short region of cytochrome *b* containing two substitutions unique to *Pterodroma* sp. 1.

PCR amplification was performed in 10 ul volumes containing 1× PCR buffer, 200 μM of each dNTP, 0.5 U of Taq DNA polymerase (Roche), 0.3 M of BSA and 0.5 μM of each primer. For all amplifications, the thermo-cycling conditions involved an initial denaturation of two minutes at 94°C, followed by 35 cycles of 94°C for 30 seconds, 50°C for 40 seconds and 72°C for one minute, followed by a final extension of ten minutes at 72°C.

PCR products were purified by digestion with one U shrimp alkaline phosphatase (SAP, USB Corp., Cleveland, USA) and five U exonuclease I (Exo I, USB Corp., Cleveland, USA) at 37°C for 30 minutes, followed by inactivation of the enzymes at 80°C for 15 minutes. DNA sequencing was performed by capillary separation at the Massey Genome Service, Palmerston North, New Zealand.

Sequences were edited in Sequencer 5.2.3 (Gene Codes Corporation). We aligned sequences from publicly available *Pterodroma* taxa (Table 2) to our own data. No indels were present in either CO1 or cytochrome *b* and sequences were aligned by eye.

Phylogenetic analyses were conducted with PAUP for maximum parsimony (MP), the PhyML v3.0 web server (http://www.atgc-montpellier.fr/phyml/, Guindon *et al.* 2010) with maximum likelihood (ML) and MrBayes v3.2.1 (Huelsenbeck & Ronquist 2001) for Bayesian analyses (BA). The short sequences obtained from the soaked bones (NMNZ S.30019 and S.35342.1) were not included in phylogenetic analyses. Analyses were performed with alignment gaps treated as missing data and Buller's Shearwater *Ardenna bulleri* (Salvin, 1888) was selected as the outgroup.

For the MP analyses a heuristic tree search was used, with 100 random addition sequence replicates and tree bisection-reconnection (TBR) branch swapping. Branch support was assessed with 1,000 pseudo-replicates. For the ML analyses the best-fit models of sequence evolution were determined for each locus using the Akaike information criterion in jModelTest v0.1.1 (Posada 2008). PhyML was run with subtree pruning-regrafting and nearest-neighbour-interchange branch swapping with ten random addition

TABLE 2

Details of DNA sequences used for this study. Corrected genetic distances (%) between Imber's Petrel *Pterodroma imberi* sp. nov., and other petrel taxa are shown for CO1 and cytochrome *b*. Taxa not referred to elsewhere in the text are as follows: Stejneger's Petrel *P. longirostris* (Stejneger, 1893), Cook's Petrel *P. cookii* (G. R. Gray, 1843), Providence Petrel *P. solandri* (Gould, 1844), Kermadec Petrel *P. n. neglecta* (Schlegel, 1863), Herald Petrel *P. a. arminjoniana* (Giglioli & Salvadori, 1869), Juan Fernández Petrel *P. externa* (Salvin, 1875), Mascarene Petrel *Pseudobulweria aterrima* (Bonaparte, 1857).

Taxon	Voucher (NMNZ)	CO1 GenBank number	CO1 genetic distance	Cytochrome *b* GenBank number	Cyt *b* genetic distance
P. imberi	S.37589.1	KT001455		KT027379	
P. imberi	S.37589.2	KT001456		-	
P. imberi	S.30019	KT001457		KT027380	
Lugensa brevirostris		AY158678	12.39	-	-
P. longirostris		JQ176028	8.45	-	-
P. cookii		GQ387307	8.45	U74345	11.27
P. nigripennis		-	-	PNU74343	8.28
P. axillaris		-	-	PAU74342	8.75
P. ultima		JF522137	10.09	JF522109	10.42
P. solandri		-	-	PSU74347	9.52
P. n. neglecta		JF522135	8.14	GQ328987	10.48
P. a. arminjoniana		-	-	GQ328979	11.07
P. alba		JQ176021	8.70	EU979352	-
P. inexpectata		-	-	PIU74346	10.78
P. sandwichensis		-	-	JF264907	-
P. cervicalis		KT001458	8.95	EU979353	-
P. externa		JQ176023	8.67	PEU74339	10.77
P. mollis	OR.22888	KT001459	2.65	-	-
P. mollis	OR.26227	KT001460	2.65	-	-
P. mollis		-	-	HQ420380	4.68
P. mollis		-	-	HQ420384	4.45
P. mollis		-	-	HQ420385	4.93
P. cahow		JQ176022	4.42	U74331	4.45
P. h. hasitata		JQ176025	4.16	U74332	4.43
P. f. feae		JX674085	3.90	FJ196356	5.25
P. f. deserta		JX674148	3.92	U74333	5.74
P. madeira		JX674273	4.67	FJ196363	4.94
P. magentae		-	-	PMU74338	4.69
P. lessonii		-	-	PLU74337	4.71
P. macroptera gouldi		E188462	4.15	EU979357	4.28
Ardenna bulleri		AB443940	15.48	AF076081	12.83
Pseudobulweria aterrima		JF522121	15.00	-	-

trees and ML-optimised equilibrium frequencies. ML branch support was assessed with 500 pseudo-replicates.

For BA, two concurrent analyses were run, each with four Markov chains of five million generations and sampling every 1,000 generations. The analyses used default priors with nst = 6 and rates = invgamma. Tracer v.1.5 (Rambaut & Drummond 2009) was used to assess stationarity, with the first 25% of samples discarded as 'burn-in' for both the combined and individual locus datasets.

Corrected pairwise distances were calculated for each locus in PAUP 4.0a136 (Swofford 2002) based on the models of nucleotide substitution selected in jModelTest. For cytochrome *b*, Phoenix Petrel *P. alba* (J. F. Gmelin, 1789), Hawaiian Petrel *P. sandwichensis* (Ridgway, 1884) and White-naped Petrel were excluded from this calculation owing to the short sequences we obtained from GenBank for these taxa. Only unambiguous nucleotides present in the entire alignments were used to calculate the distances (complete deletion), following the recommendation of Fregin *et al.* (2012).

The divergence time of *Pterodroma* sp. 1 was determined from the cytochrome *b* sequence data using BEAST 2.1.3 (Bouckaert *et al.* 2014) as described in Welch *et al.* (2014), except that priors were set to uniform. TreeAnnotator 2.1.2 was used to summarise the trees produced by BEAST and FigTree 1.4.2 (Rambaut 2012) was used to visualise the maximum clade credibility tree.

Results

For the CO1 locus, we successfully amplified and sequenced 511 bp of DNA from two fossil humeri (NMNZ S. 35789.1, S. 35789.2), 145 bp from one soaked fossil humerus (NMNZ S.30019) and 648 bp from two of the Soft-plumaged Petrel skin specimens (NMNZ OR.22888, OR.26227). For cytochrome *b* we obtained 450 bp from fossil humerus NMNZ S.35789.1 and 76 bp from fossil humeri NMNZ S.30019 and S.35342.1. No gaps or unexpected stop codons were detected and most of the variation occurred in the third codon position, suggesting that these sequences are of mitochondrial, rather than nuclear, origin.

The CO1 sequences obtained from all bones considered to be *Pterodroma* sp. 1 were identical to each other but differed from those of all other known taxa. The smallest observed corrected distance between *Pterodroma* sp. 1 and any other taxon at the CO1 locus was 2.65% to Soft-plumaged Petrel (Table 2). The cytochrome *b* sequences from *Pterodroma* sp. 1 were also identical to each other and differed from all other available sequences, with the smallest pairwise distance being 4.28% to Great-winged Petrel *P. macroptera gouldi* (Hutton, 1869) (Table 2). Genetic distances of *c.*1% for pairwise cytochrome *b* and CO1 sequences divergences are considered within the normal range for well-accepted species of petrel (Jesus *et al.* 2009, Pyle *et al.* 2011, Welch *et al.* 2014), so genetically *Pterodroma* sp. 1 is well differentiated from other known taxa. Both phylogenetic analyses indicate that *Pterodroma* sp. 1 belongs within a clade of *Pterodroma* including Soft-plumaged Petrel, Bermuda Petrel *P. cahow* (Nichols & Mowbray, 1916), Black-capped Petrel *P. h. hasitata* (Kuhl, 1820), Fea's Petrel *P. feae* (Salvadori, 1899), Madeira Petrel *P. madeira* Mathews, 1934, Magenta Petrel, Atlantic Petrel *P. incerta* (Schlegel, 1863), White-headed Petrel *P. lessonii* (Garnot, 1826) and Great-winged Petrel (Figs. 1–2). However the closest relative of *Pterodroma* sp. 1 is unclear, with it being recovered as sister to Soft-plumaged Petrel in the CO1 phylogeny (Fig. 1) but sister to a clade including Bermuda Petrel, Black-capped Petrel, Fea's Petrel, Madeira Petrel, Magenta Petrel, Atlantic Petrel, White-headed Petrel and Great-winged Petrel in the cytochrome *b* phylogeny (Fig. 2). Both relationships received only low to moderate support, so while Soft-plumaged Petrel is a fairly close relative of *Pterodroma* sp. 1, both Murphy's Petrel and Mottled Petrel—with which it was linked by Bourne (1967), Millener (1999) and Worthy & Holdaway (2002), but see Cooper & Tennyson (2008)—are more distantly related.

The divergence time estimate calculated from the strict molecular clock cytochrome *b* tree BEAST analysis indicates that *Pterodroma* sp. 1 diverged from its closest relatives around 1.37 million years ago (MYA) (95% highest posterior density 1.07–1.68 MYA; see Fig. 3). Using the same technique, the other two Chatham Island endemic *Pterodroma* species
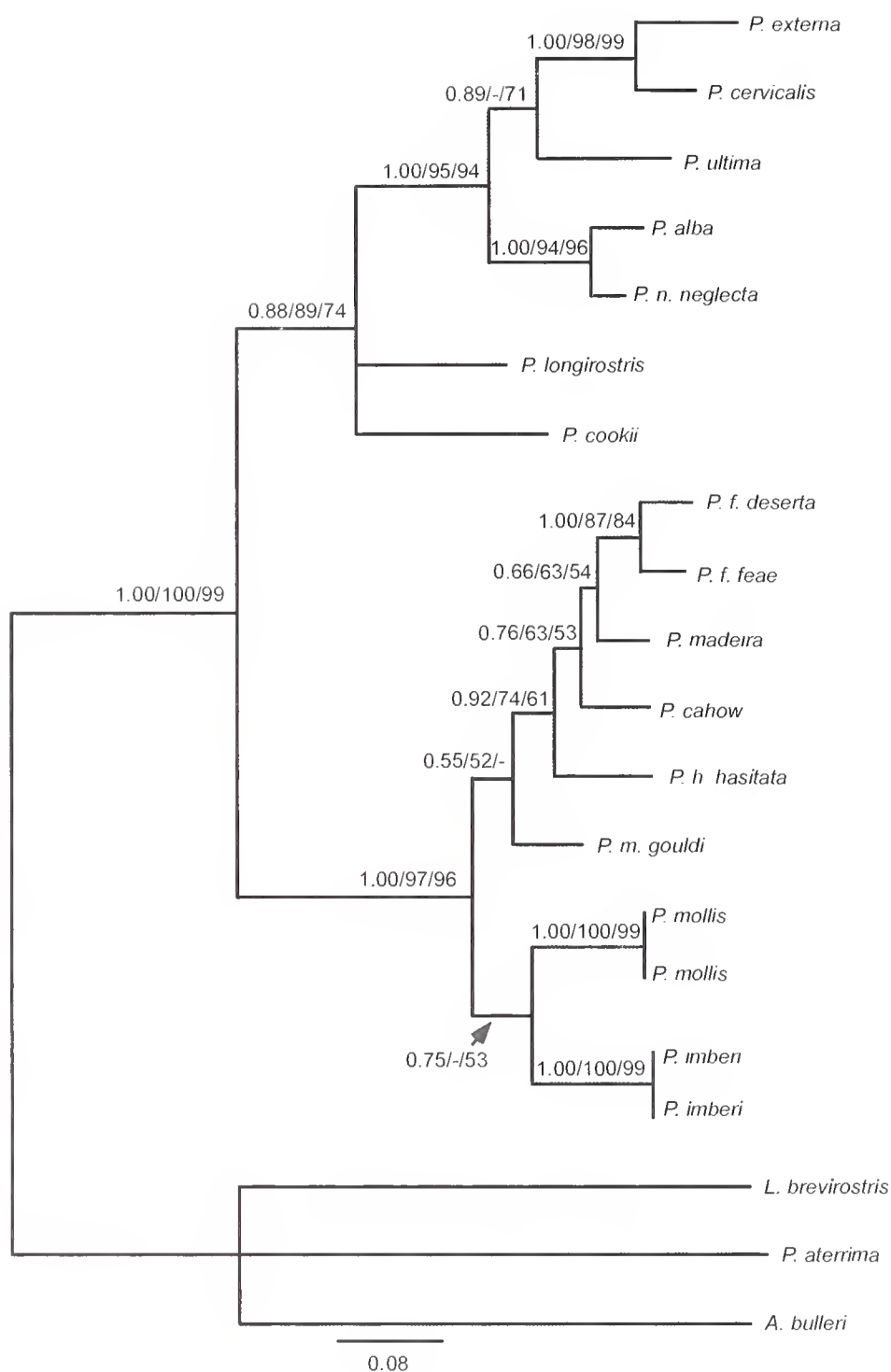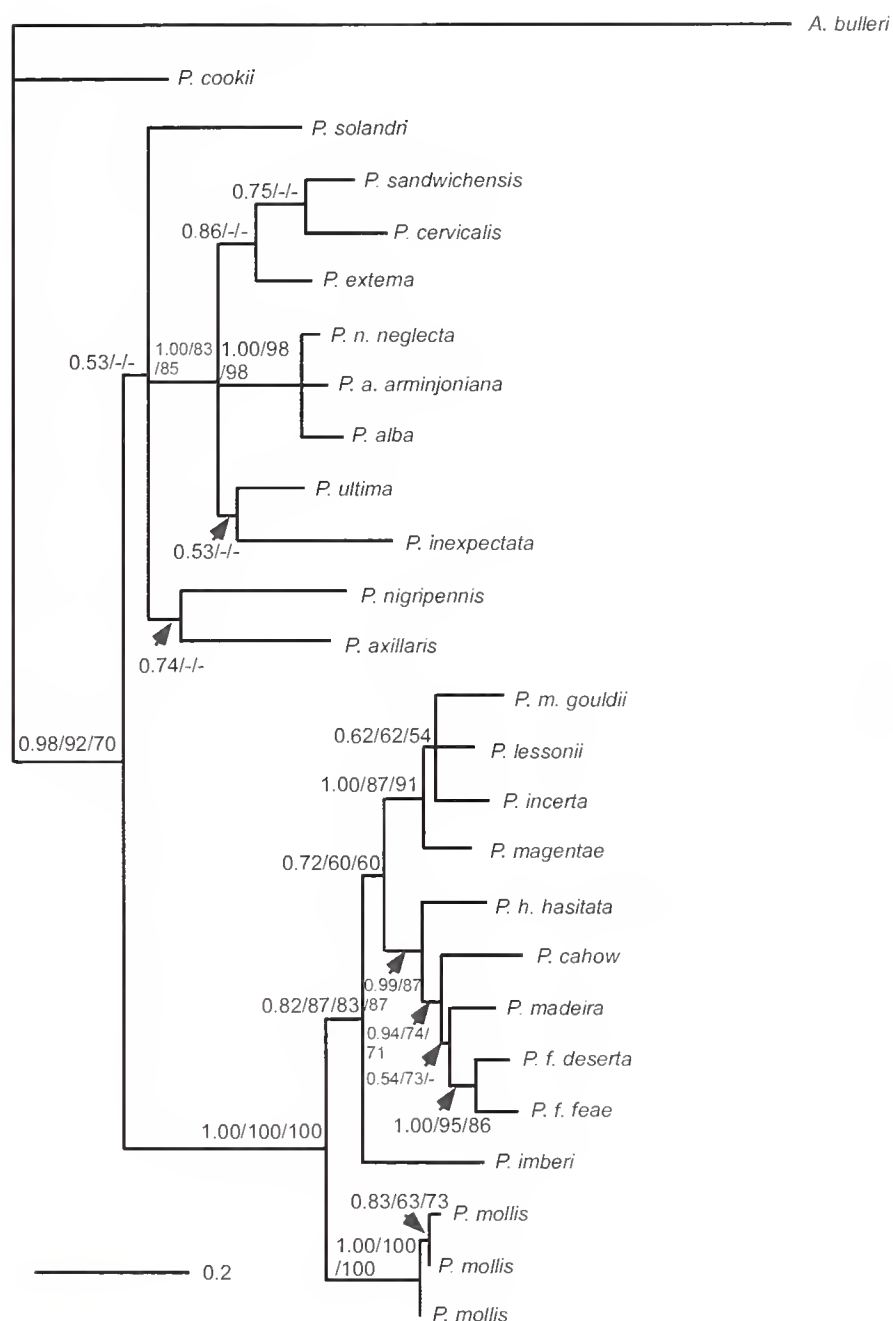
Figure 1. Bayesian consensus phylogenies constructed from CO1 sequences. Support values for nodes are as follows: Bayesian posterior probability/ maximum-parsimony bootstrap /maximum likelihood bootstrap.

diverged from their nearest relatives 1.98 MYA (*P. axillaris* from *P. nigripennis*) and 0.56 MYA (*P. magentae* from *P. macroptera gouldi*).

The combination of this genetic distinctiveness, with the previously reported morphological differences (Cooper & Tennyson 2008), strongly indicate that these bones represent an undescribed species.

NMNZ S.35342.1 was selected as a holotype because it was the best-preserved bone that yielded DNA.

Figure 2. Bayesian consensus phylogenies constructed from cytochrome *b* sequences. Support values for nodes are as follows: Bayesian posterior probability/ maximum-parsimony bootstrap /maximum likelihood bootstrap.

Systematics
Order Procellariiformes
Family Procellariidae Leach, 1820
Genus *Pterodroma* Bonaparte, 1856
Species *Pterodroma imberi* sp. nov.

   Etymology.—The species epithet is a noun in the genitive case honouring Dr Michael J. Imber (1940–2011) who had a passionate interest in the conservation, ecology and taxonomy of *Pterodroma* petrels and who undertook extensive research on the Chatham Islands.

   Holotype.—Complete left humerus (NMNZ S.35342.1) collected on 27 Feb 1992 at the Waipawa Stream mouth, Pitt Island, Chatham Islands (map grid reference NZMS 260 Chatham Islands sheet 2 739160), by Rhys Richards, Holocene age. See Fig. 4.
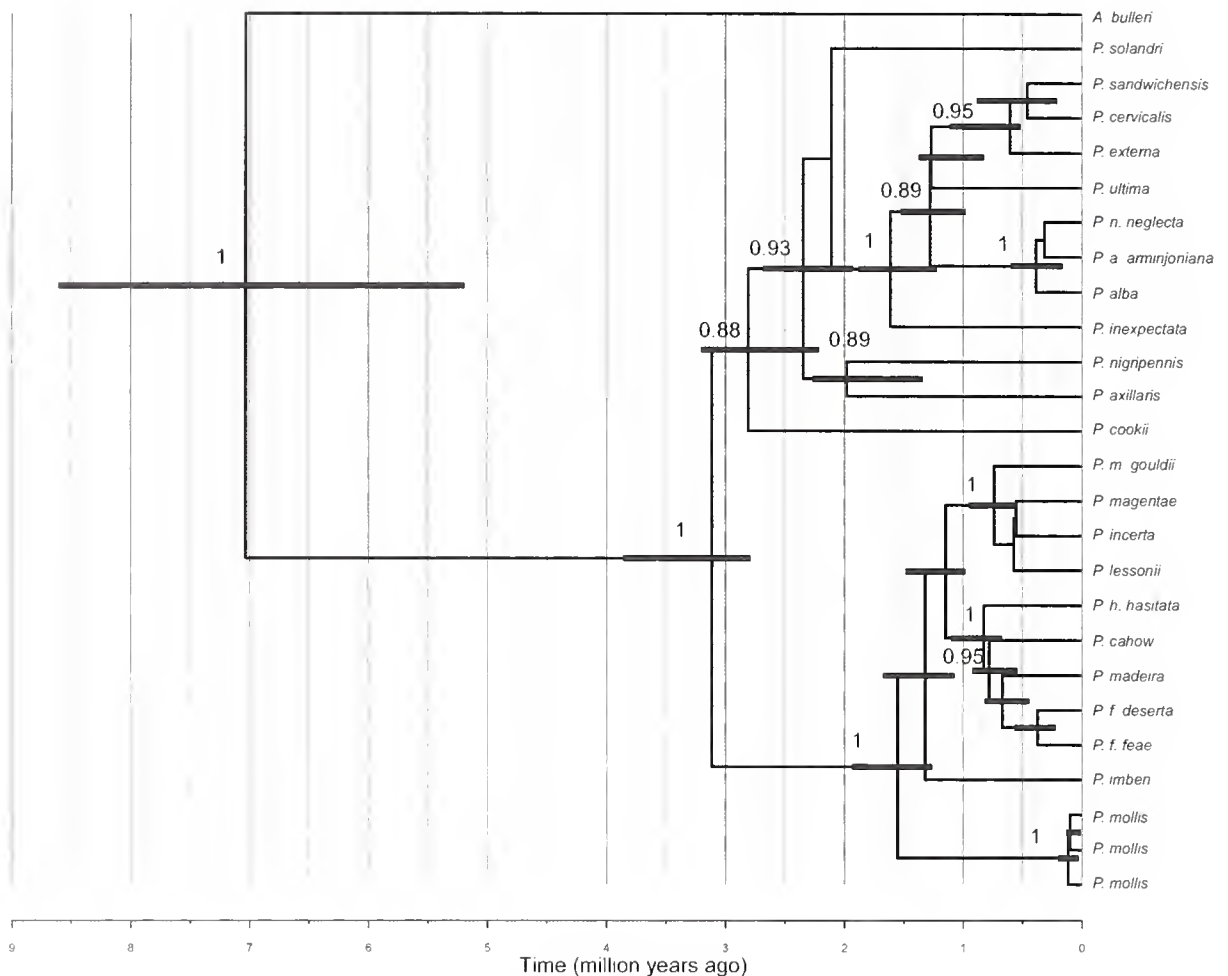
Figure 3. Maximum clade credibility tree from the BEAST analysis of *Pterodroma* cytochrome *b* sequences. Nodes are posterior mean ages (MYA), with node bars representing the 95% HPD intervals.

Measurements of holotype.—Max. total length 86.3 mm, max. proximal width *c.*20.7 mm, max. distal width (including the processus supracondylaris dorsalis) 13.4 mm, mid-shaft width 5.6 × 3.9 mm.

Paratypes.—All other humeri that have been successfully sequenced for DNA: NMNZ S.30019, NMNZ S. 35789.1, NMNZ S. 35789.2; the collection details for these specimens are presented in Table 1.

Distribution of species.—Extinct. Formerly common and widespread on Chatham, Pitt and Mangere Islands, Chatham Islands, New Zealand (Cooper & Tennyson 2008).

Suggested vernacular English name.—Imber's Petrel.

Diagnosis.—A medium-sized *Pterodroma* species with a median humerus length of 86 mm (averaging slightly larger than that of Mottled Petrel and Soft-plumaged Petrel: Cooper & Tennyson 2008). Other elements that probably belong to Imber's Petrel suggest that the other main limb bones were also slightly larger than those of Mottled Petrel and Soft-plumaged Petrel but that the tibiotarsus was proportionately longer in Imber's Petrel (Cooper & Tennyson 2008). The skeletal proportions of Imber's Petrel appear to differ from all other *Pterodroma* species occurring in the New Zealand region (Cooper & Tennyson 2008).

Extant *Pterodroma* taxa from outside the New Zealand region and similar in size to Imber's Petrel do exist (e.g. Phoenix Petrel, Fea's Petrel *P. f. feae*, Fea's Petrel *P. f. deserta* Mathews, 1934, and Madeira Petrel; see Brooke 2004) but none are genetically close relatives.

Figure 4. Holotype left humerus of *Pterodroma imberi* sp. nov., NMNZ S.35342.1. © Te Papa. 4A. caudal view. 4B. cranial view.

There are three described extinct *Pterodroma* species but none is closely related to *P. imberi*. *P. rupinarum* Olson, 1975, from the Pleistocene (and younger) of St. Helena, in the South Atlantic Ocean, is a similar-sized bird (Olson 1975) but is placed within a clade of petrels distributed in the North Atlantic, and most closely related to Fea's Petrel based on cytochrome *b* sequences (Welch *et al.* 2014). *P. kurodai* Harrison & Walker, 1978, from the Pleistocene of Aldabra Atoll, Indian Ocean, is notably smaller than Imber's Petrel (Harrison & Walker 1978), and *P. jugabilis* Olson & James, 1991, from the Holocene of Hawaii is even smaller (Olson & James 1991).

Discussion

The genus *Pterodroma* is diverse with a high number of taxa endemic to islands and several taxa threatened with extinction (Brooke 2004). The Chatham Islands have two surviving but endangered endemic species, Magenta Petrel and Chatham Petrel; the remains of both have been found alongside those of Imber's Petrel in fossil dune sites. Imber's Petrel was intermediate in size between these two species and presumably filled a separate ecological niche. The 20th century colonisation of the New Zealand subantarctic region by the similarly sized Soft-plumaged Petrel (Tennyson *et al.* 2013) may be related to an ecological niche becoming available in the region as the result of the extinction of Imber's Petrel. There is evidence that Imber's Petrel may have survived into the late 19th century (Tennyson & Millener 1994) but there are no known records of it alive.

The extinction of Imber's Petrel was undoubtedly a result of human colonisation of the Chatham Islands, beginning *c*.400–700 years ago (Wood *et al.* 2014). Human hunting, combined with the impacts of other introduced mammals, are the probable causes of its extinction. Likely key predators on Chatham Island were Pacific Rats *Rattus exulans*, Ship Rats *R. rattus*, Norway Rats *R. norvegicus* and feral cats *Felis catus*. Cats are present on Pitt

Island but rats have never established there. Human hunting may have contributed to its decline on Mangere Island but cats are the likely cause of its final demise (Tennyson & Millener 1994).

The estimated divergence times of the three endemic Chatham Island *Pterodroma* species from their nearest relatives, based on the cytochrome *b* gene tree, range from 1.98 MYA to 0.56 MYA. These dates are what might be expected for endemic birds on an archipelago that has been emergent for only *c*.2.5 million years (Campbell 2008).

The formal description of Imber's Petrel adds yet another extinct bird, and the first *Pterodroma* species, to the list of human-caused extinctions in the New Zealand archipelago (Holdaway *et al.* 2001, Boessenkool *et al.* 2009, Williams *et al.* 2014, Wood *et al.* 2014).

While DNA has been soaked from modern bones (e.g. Asher & Hofreiter 2006) and teeth (Rohland *et al.* 2004) previously, the soaking extraction method presented here provides a non-destructive technique for obtaining DNA from Holocene fossils. Our trials with multiple fossil bones from different species (LDS & AJDT unpubl. data) have shown that our soaking method is less successful at yielding DNA than the method of removal and digestion of bone fragments. However, it is a useful technique for extracting DNA from particularly valuable specimens, such as types or those of rare species, as it minimises overall morphological damage. When applying this method to other taxa, it is likely that the soaking time will need to be varied according to the size of the bones. Contamination may also be more likely with this method because the outer surface of the bone is not removed prior to DNA extraction. We suggest following the recommendations made by Gilbert *et al.* (2005) in assessing whether results obtained through soaking are likely to be genuine or contamination.

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First nesting record of Band-winged Nightjar *Systellura longirostris* in Uruguay

by Jeremy K. Dickens, Thiago V. V. Costa, Henry Dario F. Machado & Enric Fontcuberta

The natural histories and distributions of many Neotropical nightjars are still very poorly known due to their cryptic behaviour and habits. Band-winged Nightjar *Systellura longirostris* is a mid-sized species, widespread over much of South America, except the north-west (Cleere 1998). It exhibits considerable vocal and morphological variation between populations, suggesting that multiple species are involved, a fact supported by a recent molecular study (Sigurdsson & Cracraft 2014). The nominate subspecies occurs along the Atlantic coast of Brazil, from Bahia to Rio Grande do Sul, as well as in Paraguay, eastern Argentina and most of Uruguay (Cleere 1998, 1999). However, aspects of its breeding biology are still poorly understood.

Figure 1A. Bichadero-Froz, Cuchilla de Laureles, Tacuarembó, northern Uruguay, July 2014 (Jeremy K. Dickens); (B) male Band-winged Nightjar *Systellura longirostris*, Bichadero-Froz, Cuchilla de Laureles, Tacuarembó, northern Uruguay, July 2014 (Henry Dario Machado)

Figure 2. Nesting Band-winged Nightjar *Systellura longirostris*, Bichadero-Froz, Cuchilla de Laureles, Tacuarembó, northern Uruguay: (A) female and ecloded eggs, September 2013; (B) nestlings, October 2013 (Henry Dario Machado)

We present the first report of *S. longirostris* nesting in Uruguay, with a description of eggs and nestlings. A nesting *S. longirostris* was recorded in September–October over two consecutive years (2012–13) at Bichadero-Froz, Cuchilla de Laureles, Tacuarembó, northern Uruguay (31°21′34.2″S, 55°59′4.8″W). Habitat comprised rocky outcrops, with several small streams, at the edge of a densely forested gorge in an area otherwise characterised by heavily grazed open pampas (Fig 1A). In late September 2013, the nest possessed two nearly pure white eggs, with several almost imperceptible pale brown spots. These were incubated by the female when photographed (Fig. 2A). The eggs were laid on a patch of soft lichens and bryophytes, with a few pebbles, and not directly onto the bare rock. It was unclear whether the pebbles in the nest were naturally present or if they had been placed there by an adult. On the next visit, *c.*10 days later, in early October, two pale tan-brown nestlings were observed at exactly the same spot (Fig. 2B). In July 2014, two *S. longirostris* were found roosting together during the day on the rocky outcrop at Bichadero-Froz. The first, a male, was photographed (Fig. 1B) and, when flushed, flew into the gorge and took cover in the forest with the second, which was identified as a female but was not photographed. This male had an unusual rufous plumage, superficially similar to Rufous Nightjar *Antrostomus rufus*, but was identified using the following traits: somewhat uniform upperparts, without any conspicuous scapular pattern; dark remiges with a semi-concealed buff band; and the fairly extensive white tips to the inner webs of the two outermost rectrices (visible in the photo). The incubating female also had an atypical, pale, plumage, but the overall pattern of the upperparts, with no conspicuous markings on the head, nape and scapulars, ensures its identification.

The breeding season coincides with that already reported for this subspecies, September to December, with the only previous data coming from records in Rio de Janeiro (Sick 1997) and Minas Gerais (Hoffmann 2010), in south-east Brazil, and in Santa Fé province, Argentina (de la Peña 2006). Egg and chick coloration and clutch size are also similar to those mentioned in the literature. However, they differ from the other nesting records by being laid onto a soft substrate, not bare rock, and hatching via the middle of the egg, not the broader end. Their breeding at the same locality in two consecutive years and presence in a third is suggestive of nest-site fidelity. This study reinforces the need for

additional studies on the breeding biology of Neotropical nightjars, especially for species whose taxonomy is unclear and comprise various vocally and/or morphologically distinct forms, such as *S. longirostris*.

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